An Introduction To
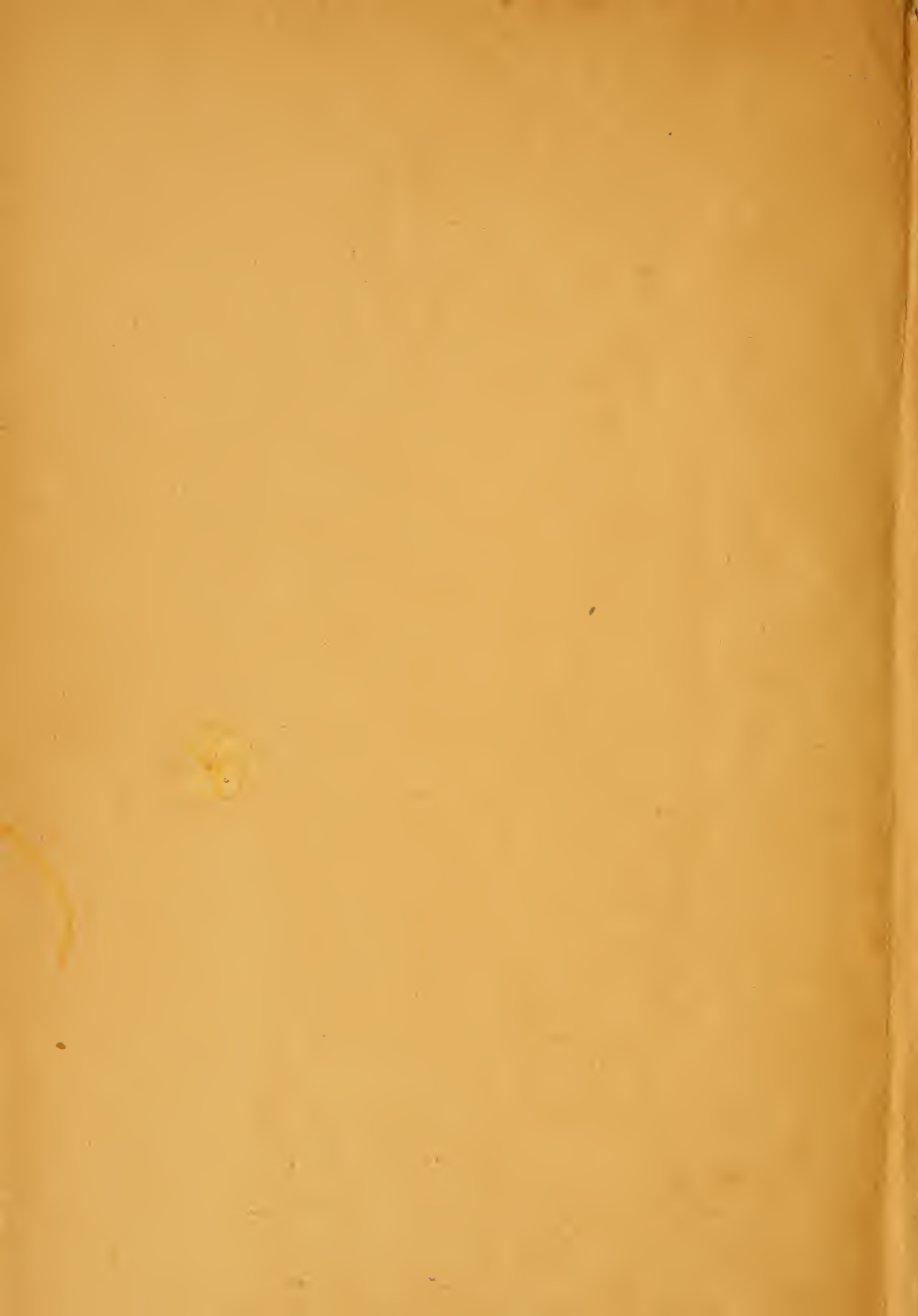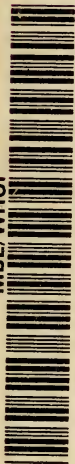# The Genetics Of
Habrobracon Juglandis Ashmead

ALBERT MARTIN, JR.

An Introduction To
The Genetics Of
Habrobracon Juglandis Ashmead

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TO MY WIFE
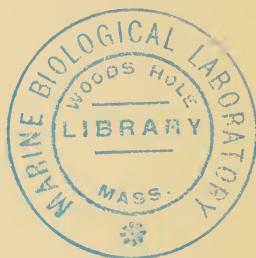
FOREWORD

This summary is designed for students of Habrobraconology. Although written primarily for use in course work, it is hoped that it may serve as a reference for those engaged in experimental genetics. The aim of the work has been to present a clear and readable account of the results of investigations made thus far in the genetics of Habrobracon juglandis (Ashmead).

The insect is described, and its method of culture as well as that of its host is outlined in detail. A complete list of extant and discarded mutant types is included. The statistical formulas utilized in determining crossover values and other linkage problems are presented. Tables in the appendix summarize present linkage information and effects of X-radiation. A glossary and a complete bibliography of Habrobraconology accompany the summary.

I am deeply indebted to Professor P. W. Whiting, of the University of Pennsylvania, for reading the manuscript and for making valuable suggestions, and to Dr. G. M. McKinley, of the University of Pittsburgh, for his encouragement. Special thanks are given to my wife, Dr. Phyllis C. Martin, of the Pennsylvania College

for Women, who read the text at several stages
in its preparation, and assisted in the clari-
fication of the language.

<div align="right">Albert Martin Jr.</div>

University of Pittsburgh
        May, 1946

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Chapter I

INTRODUCTION

For the purpose of studying inheritance, the insects have been of primary importance, chiefly because their life cycle is short, and because they produce large numbers of progeny. The fruit-fly, Drosophila melanogaster, and the bee, Apis mellifica, have been studied intensively by a number of workers; but the parasitic wasp, Habrobracon juglandis (Ashmead), has been given special study by P. W. Whiting and his co-workers during the past thirty years.

Habrobracon is a parasitic hymenopteran of the superfamily Ichneumonoidea, family Braconidae, subfamily Vipiinae, genus Microbracon, species hebetor (Say) (Muesebeck, 1925). The species M. hebetor, was first described in 1836 by Say who, however, called it Bracon hebetor. Later that same year he described another species, which he called B. dorsator. The species, B. hebetor and B. dorsator, are now known to be the same. Many other names have been applied to this insect since the original ones proposed by Say: B. brevicornis (Kirby, 1884; Marshall, 1885), B. juglandis (Ashmead, 1889), Habrobracon hebetor (Johnson, 1895), Bracon (Habrobracon) honestor (Riley, 1895; Howard, 1895), Habrobracon beneficientior (Viereck, 1911), H. brevicornis (Cushman, 1914; P. W.

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Whiting, 1918, 1921e), and H. juglandis (Cush-
man, 1922).

The type specimens of Bracon hebetor (Say)
and of B. dorsator (Say) have been lost, but
those of B. juglandis (Ashmead), and Habrobra-
con beneficientior (Viereck) are in the United
States National Museum, Washington, D. C., the
former bearing type catalogue number 2913, the
latter, number 13494.

The species, Microbracon hebetor (Say), is
exceedingly close to M. brevicornis (Wesmael),
and the two have been much confused in litera-
ture. In early papers on the genetics of
Habrobracon juglandis, the name, H. brevicornis
(Wesmael) was used. Cushman (1922) cleared up
this matter, calling attention to the differ-
ence in habit between the two species, and
pointing out some morphological differences.
Habrobracon brevicornis is known to parasitize
the European corn-borer, Pyrausta nubilalis,
while Habrobracon juglandis parasitizes the
Mediterranean flour moth, Ephestia kuehniella
(Zeller). The females of Microbracon hebetor
are readily distinguished from those of M.
brevicornis by the antennae, which consist of
13-15 segments in the former, and 17-19 seg-
ments in the latter. At this time, however,
Cushman did not regard Bracon juglandis (Ash-
mead) as identical with B. hebetor (Say). It
appears, after a careful consideration of Say's
description of B. hebetor, that there can be no
reasonable doubt that Say and Ashmead were
dealing with the same species (Muesebeck, 1925).
The name Hadrobracon brevicornis (Wesmael) was
used by Doten (1911) in describing the relation
of food to reproduction and longevity in cer-

tain hymenopterous parasites, and by Cushman (1914), and P. W. Whiting (1918, 1921e) in their work with Habrobracon juglandis. This use of Hadrobracon is clearly a misspelling since no such generic name is recognized in scientific literature (Neave, 1939). There have been some genetic studies reported on Microbracon brevi-cornis (Wesmael) (Speicher and Speicher, 1940) and M. pectinophorae (Watanabe) (Inaba, 1939, 1940) under the generic name, Habrobracon. The present account, however, deals mainly with the work done on the genetics of Microbracon hebe-tor (Say), but since the name Habrobracon juglandis (Ashmead) has been used as a synonym for Microbracon hebetor (Say) and is so well entrenched in genetic literature, it is prefer-able to use it in a work of this kind.

At present five wild-type stocks of Habro-bracon juglandis are being reared by Whiting for genetic studies. These stocks have been named for the geographic locality in which they were found, and have been arbitrarily numbered to differentiate one from the other in genetic crosses. Thus wild-type stock number one (1) is from Lancaster, Pennsylvania, stock number eleven (11) from Iowa City, Iowa, stocks number thirty-two (32) and thirty-three (33) from Cal-ifornia, and stock number twenty-five (25) from New York City, New York.

Habrobracon juglandis is ecto-parasitic on various cereal-infecting caterpillars. Refer-ences in literature to Bracon or Habrobracon brevicornis, Microbracon hebetor, or Habrobra-con juglandis as parasites of the Mediterranean flour moth, Ephestia kuehniella (Zeller) (Wash-burn, 1904), of the meal moth, Plodia inter-

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punctella (Grandi, 1931), the fig moth, Ephes-
tia cautella (Walker) (Simmons and Reed, 1929)
and of the bee moth, Galleria mellonella, con-
cern this species. Habrobracon is distributed
throughout the world wherever its hosts, par-
ticularly the flour and meal moths, are present
(Fahringer, 1928; Goidanich, 1934; Muesebeck,
1925; Watanabe, 1935). It does especially well
in laboratory cultures if raised on the cater-
pillars (larvae) of Ephestia kuehniella. The
original Lancaster (1) stock was derived from
seven females bred from a single infested
Ephestia caterpillar and mated to their sons in
June, 1919.

Genetic research with Habrobracon was begun
at the University of Pennsylvania in the fall
of 1916 by P. W. Whiting. The first mutant
type, a recessive orange eye color, appeared
March 27, 1920 (P. W. Whiting, 1921c). Tests
made with this first mutant indicated that
three types of individuals occur regularly in
the species where the parents are related.
Males arise from unfertilized eggs, and are,
therefore, haploid and display only maternal
traits; females develop from fertilized eggs,
and, therefore, may show both maternal and pa-
ternal characters. In a few cases diploid males
have appeared (P. W. Whiting, 1921e). These
may be recognized because they show paternal
characteristics. Habrobracon is, therefore,
typical of the order, in that it reproduces
both gamicly and parthenogenetically.

Habrobracon illustrates complete metamorpho-
sis and furnishes rich material for experimen-
tation because of the striking effect of temper-
ature on its body color, its habit of parasit-

ism, its parthenogenetic method of producing
haploid males, the occurrence of gynanders and
other genetic mosaics, its impaternate or par-
thenogenetically produced females, and its in-
heritance of easily distinguished mutant traits.
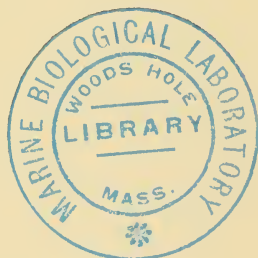
Chapter II

DESCRIPTION

Habrobracon juglandis in the adult stage is approximately three millimeters in length. Variations in size are directly related to the quantity of food available to the larvae. General body coloration varies from honey-yellow to jet black, depending largely upon the temperature during development. Females are, in general, less deeply pigmented than males in any given strain. Body colors are similar on dorsal and ventral sides of head and thorax. The distribution and quantity of integumental. pigmentation are exceedingly variable, but normally produced individuals are bilaterally symmetrical. The color pattern of the praescutum, scutum, mesoscutellum, and the dorsal plate of the mesophragma is used in classifying degrees of pigmentation since it is consistently related to muscle areas and is not complicated by other factors. There is a high degree of asymmetry of pigmentation in specimens mosaic for mutant factors and for sex. As compared with females (Fig. 1), males (Fig. 2) have longer antennae. The antennae consist of a scape, and a pedicel, in the males a flagellum of 20 to 22 segments, and in the females a flagellum of 13 to 15 segments. The males have larger ocelli, smaller wings and legs, and larger compound
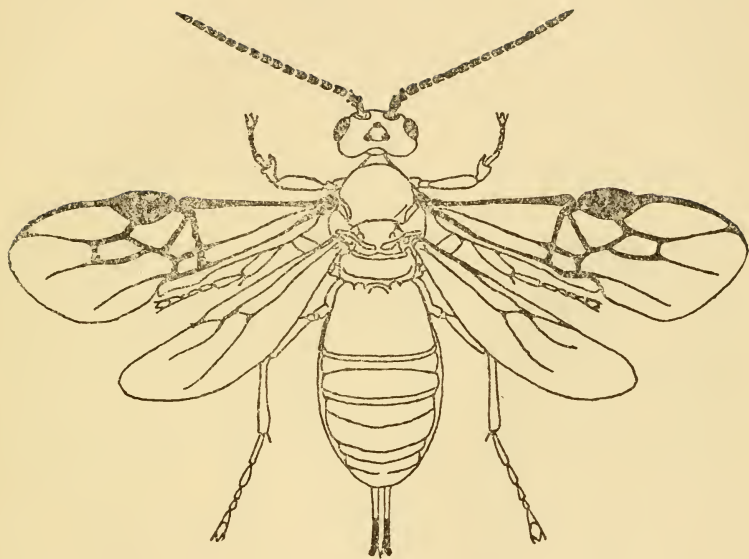
Fig. 1.   Dorsal view of <u>Habrobracon</u> female.

X 18.

Fig. 2. Dorsal view of <u>Habrobracon</u> male.

X 18.

eyes, although the facets of the ommatidia
closely approach those of the females. The
wing size of a normal specimen varies consider-
ably along with differences in general body
size. Measurements from tip of sclerite at
base of costa to end of radius vein on the cos-
tal margin vary from 2.04 to 2.35 millimeters
for female wings and from 1.89 to 2.30 for male
wings. These figures make it clear that, while
males have slightly smaller wings than females,
variations which normally occur within each sex
are such that measurements are ordinarily of no
avail for sex identification. The microchaetae,
however, may be used to differentiate diploid
males from haploid males and diploid females,
since each bristle on the wing corresponds to
and gives indication of the presence of a wing
surface cell which is larger in diploid males
than in haploid males or diploid females (Spei-
cher, 1935; Grosch, 1945). Males also have
smaller abdomens with abdominal sternites small-
er and thinner than those of females. Abdomi-
nal tergites, especially the first and second,
are thinner in the males. A transverse sub-
basal depression is evident especially on the
fourth and fifth tergites of the males. In all
types the abdomen is covered, ventrally and
laterally, by a cuticle which is thin and trans-
parent except for small sclerotized regions at
the lateral ends of the abdominal sternites.

Female genitalia consist of a pair of elon-
gate sensory gonapophyses blackened distally, a
brownish sting, and a vagina anterior and ven-
tral to the gonapophyses. The paired gonads of
Habrobracon females each consist of two ovari-
oles morphologically composed of three regions:

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(1) dorsal, apical end-chamber with oögonia, followed by (2) masses of nurse cells alternating with (3) developing oöcytes each of which is surrounded by follicle cells. In mature females which have fed upon host caterpillars the lower end of each ovariole is expanded into a storage chamber (uterus) in which there are from two to five eggs with chorion and yolk fully developed and with follicle cells still present but with nurse cells gone. In females about to emerge from the cocoon the uteri are small and empty. The first maturation division is initiated before oviposition. Speicher (1936) showed that when the egg reaches the uterus, acquires a chorion, and loses its nurse cells, its nucleus increases in size, and the chromatin elements appear. They quickly shorten and with the disintegration of the nuclear membrane move to the center of the nuclear area and become arranged on a flat metaphase plate. A spindle forms at the same time. The chromosomes continue to late metaphase stage, and here maturation is stopped until after oviposition. Oviposition will not occur unless the female has fed upon the host caterpillar. Within the nuclei of the younger oöcytes the earlier processes of the meiotic prophase are going forward.

The genitalia of the male consist of an outer and an inner pair of claspers and a penis. In normal haploid males the paired, rounded, yellowish testes (about one-fourth millimeter in diameter) are fused and lie dorsally to the intestine in the posterior part of the body. Each gives off a lateral duct which passes around the intestine and unites with the acces-

sory gland to form a common duct which connects
with the penis. Internally the testes are sub-
divided into a number of cysts. Scattered
throughout the testes of immature individuals
are spermatogonial cells many of which are in
compact rosettes. Some are in larger, looser
rosettes. In the gonads of late pupae matura-
tion division figures and even some spermatids
may be observed, but gonads of freshly eclosed
males show the highest percentage of cells in
active division and have, therefore, been stud-
ied most intensively.

Definite types of reactions characteristic
of sex are found in Habrobracon. The females
sting the host caterpillars on which they sub-
sequently feed and lay their eggs. The males
are entirely indifferent to caterpillars, but
they show characteristic reactions towards fe-
male wasps, such as flipping wings, mounting,
and beating with wings and antennae in the proc-
ess of mating.

Chapter III

CULTURE

Habrobracon juglandis has proved to be excellent material for laboratory study and research investigations because of the ease with which it can be handled, the low cost of feeding the stocks, and its brief ten-day generation period. ·These factors together with its fecundity make possible the accumulation of large numbers of progeny in a short time.

Habrobracon is cultured in shell vials, twenty millimeters by seventy millimeters, plugged with cotton covered with fine mesh cheese-cloth through which neither caterpillars nor wasps will burrow. When the wasps are cultured in this manner it is possible to observe the mating procedure and the complete life cycle. After mating, the female is given one caterpillar of the host, Ephestia kuehniella, and incubated at 30° C. After stinging the caterpillar the female sucks juice from the puncture but deposits no eggs until her victim has become torpid. Young females are given only one caterpillar at first because they do not always sting immediately, and the caterpillars, if not stung, start to spin webs upon exposure to incubator temperatures. The caterpillars may in this way escape being stung by the wasp, or the wasp may become trapped in the web and be killed by the

caterpillar. After a wasp has once stung cat-
erpillars and oviposited, she usually stings as
soon as she is confronted with fresh caterpil-
lars, and as many as five can be given at once.
Female wasps feed on the juice which is essen-
tial to reproduction. This is borne out by the
fact that females will not lay eggs until they
have fed upon a stung caterpillar, although
they may be kept alive for weeks on diluted
honey. On the other hand, Habrobracon males
subsist on a diluted honey diet entirely and
will not feed on caterpillar juice even when it
is available. Both the males and the females
may be kept alive in shell vials for extended
periods by feeding on a mixture of honey and
water. It is convenient to keep the honey and
water in separate small containers, for if the
two are mixed, fermentation occurs. A metal
rod such as a dissecting needle or a dental
probe is dipped into the honey, then into the
water and touched to the inside of the vial
where the drop will adhere. At ordinary room
temperature it is necessary to feed the wasps
every other day, but if it is desired to keep
any individuals isolated for an extended period
it is better to feed them once and set them in
the ice chest at approximately 10° C.

Following the stinging of the caterpillar,
the female, if mated, deposits both fertilized
and unfertilized eggs on top of or on the under
side of the caterpillar; if a virgin, only un-
fertilized eggs will be laid. These eggs may
be easily observed. If it is desired to study
the ovipositing wasps or to count their eggs
the paralyzed caterpillars are placed upon a
piece of glass which is set about three-fourths

of an inch above a mirror. Then by focusing
either upon the insect directly or upon the
image, upper or lower sides may be observed.
There is no danger of contamination from the
food even if wasps have infested the caterpil-
lar culture for eggs are never laid except upon
torpid and flaccid hosts. Such should, of
course, be discarded in selecting caterpillars
for the culture vials.

An occasional female lays many sterile ova.
Data on eggs of such exceptional females are
not included in general summaries. There is
likewise a tendency on the part of many females
to lay "shells," apparently filled only with
fluid. This soon evaporates, and the egg be-
comes brittle. In one series (A. R. Whiting,
1940a) the percentage of such "shells" was 2.26
for the first ten days of life of the females
and 12.06 for the second ten days. Some females
produced no "shells," although all were from
the same inbred line. Those "shells" are like-
wise omitted in computing hatchability ratios.
It has been thought that the "shells" might be
the result of the females stinging their eggs.
It has been concluded that females sting eggs
very rarely if at all, and that stung eggs can
continue development after such injury. In or-
der to determine the time of death of eggs
which, for various reasons, do not hatch, the
eggs may be collected at intervals and placed
in the mineral oil, "Nujol," where development
proceeds normally and conditions can be clearly
observed.

The developmental limits for the egg have
been found to be 12-38° C. at a relative humid-
ity of 76-98 per cent (Maercks, 1933). The

life cycle is completed in the shortest time at 33.5° C. and a relative humidity of 32-98 per cent. The optimum temperature is, however, 29-30° C. with a relative humidity of 80 per cent. The temperature optimum is considered to be the temperature at which there is 0 per cent mortality and the smallest variation in the effect of various percentages of relative humidity. The relative humidity optimum is found on the humidity scale at the point where there is the greatest range of temperature with the same mortality. The duration of development is influenced especially by temperature and only slightly by relative humidity. At the temperature optimum the mortality is not influenced by slight deviations from optimum humidity, but at non-optimal temperatures, either high or low, there is an increase in mortality the farther the temperature and humidity are removed from the optimum. The mortality at non-optimal temperatures is influenced considerably by humidity; however, the duration of development of the survivors is less affected.

At optimum or near optimum conditions, the deposited eggs hatch into larvae in two or three days. The larvae feed on the juice of the host caterpillar and grow to the size of two to five millimeters depending upon how much food is available. These maggot-like larvae upon emergence cling to the integument of their host.

About three days after setting, or when larvae are present on the caterpillars, the female should be transferred to a new vial and given fresh caterpillars. A small camel's hair brush is useful in making such transfers, as the wasps

tend to cling to the sides of the vial and must be brushed off into the new vial. Transfer at three day intervals is continued until the female dies.

The larval stage lasts about two days, at the end of which time the larvae spin cocoons with silk from the salivary glands. The cocoon entirely surrounds the larva, but only a very thin layer of threads is laid down where it adheres to the inner surface of the vial; thus it is possible to watch the development of the pupa from this side. The caterpillars by this time are reduced to shrivelled remnants which may be removed from the vials.

In the higher hymenopterans the end of the stomach is closed during larval life. The fecal matter is, therefore, retained in the stomach until pupation and then discharged into the end of the pupal case. This discharge appears as a dark brown mass and marks the posterior end of the developing pupa.

After two days, the pupa changes externally from the worm form of the larva into approximately adult insect form. Legs and wings are not fully formed until the third day of pupal existence when pigmentation and sclerotization take place rapidly. Compound eyes are formed externally by the end of the second day, but the internal tissues are not completely developed until the third day, and facets are not apparent until the wasp is almost ready to hatch. Near the end of pupal life the thorax and antennae become deeply pigmented. The time of pupal life varies somewhat, but most wasps average about four days.

In three day pupae, the ventral side lies

squarely under the thin attached layer of the
cocoon. Antennae are folded down the ventral
side, and in females they reach to about the
posterior end of the thorax; in males, they ex-
tend to about the second sternite of the abdo-
men. The sexes may be readily separated by
observing the long antennae of the males and
the prominent sting and sensory gonapophyses of
the females.

At eclosion both males and females are ei-
ther mature sexually or almost so; consequently
females are certainly virgin only if males are
not present. In obtaining virgin females, pupae
should be isolated, or great care should be
taken to see that no mature wasps are present
in the culture. These insects have the habit
of crawling back into the cocoons after eclo-
sion. For this reason it is important to see
that cocoons are either empty or intact.

Since virgin females are often necessary in
experimental work, methods have been devised
for obtaining them in numbers and with a mini-
mum of attention. The method that has proved,
most successful is also the simplest. Cater-
pillars are stung by females of any kind. The
females are removed before any eggs are laid.
Then about five stung caterpillars are spread
out along one side of a shell vial, and the
mated female that is to be the mother of the
desired virgins is placed in the vial with them.
The vial is laid on its side and kept in that
position. The female then lays her eggs on the
caterpillars, the larvae hatch from them and
feed, and when they are ready to pupate, they
crawl off the host caterpillars and spin their
cocoons on the side of the vial instead of pil-

ing up on each other as they would if the vial were kept upright. As they develop into mature wasps, they can be observed through the vial by means of a hand lens or a binocular dissecting microscope, and as the sex becomes evident, the males or any questionable pupae may be killed with a needle, thereby insuring the eclosion of virgin females only.

If it is necessary to rear all the progeny but still to retain the females as virgins, another method is effective. This consists of placing the caterpillars and wasp larvae on cellophane discs placed in petri dishes. When the larvae have pupated, the sex of the pupae may be determined by viewing them from the under side of the cellophane by means of a hand lens or a microscope. The sexes may be separated by cutting the cellophane surrounding them, and the males and females may be placed in separate vials to await eclosion.

Various non-genetic influences affect the ratio of offspring. Sperm supply in the seminal receptacles influences the female ratio. Production of females tends to be somewhat reduced in later culture vials preceding their total absence after exhaustion of sperm supply. Matings with old males result in lower female ratios than matings with young males, probably because of lowered sperm supply. In much of the earlier work, entire fraternities were summarized including the haploid males produced after depletion of sperm. Ratios thus obtained are subject to great variation. They depend in large measure on the length of life of the mothers, who may die before they have exhausted

their supply of sperm received from the initial mating, or who live for many days afterward.

The average size of fraternities varies according to length of life of the mother and the technique of the investigator, being reduced by poor cultural conditions such as small size, scarcity, or disease of the host caterpillars, overcrowding and presence of recessive lethals or semilethals, as well as by crossing between related stocks (close-crossing). Average offspring per day or per vial may be determined for individual females or for groups of females. The average number of fertilized eggs and hence females per vial or per fraternity may be twice as high in crosses between unrelated stocks (outcrosses) as in close-crosses. The number of eggs remaining unfertilized and hence the average number of haploid males will be unaffected, except for crowding in the larger, outcross fraternities.

To facilitate the counting of Habrobracon progeny, it is necessary to etherize and to examine the anaesthetized individuals under a binocular dissecting microscope at about twenty diameters magnification. Since Habrobracon is much more resistant to ether than is Drosophila, it is usually safe to allow one group of wasps to remain in the etherizing bottle while another group is being counted. For anaesthesia two wide mouthed bottles are used. A cork with cotton suspended on a wire and saturated with ether may be transferred from one bottle to the other. One group of wasps is placed in one of these wide mouthed bottles and etherized while those from the other bottle are being counted and examined. After examination the wasps may

be returned to their shell vial, destroyed by dropping them into a jar of mineral oil, or preserved for future use.

Preserving fluid is nine parts of 95 per cent alcohol to one part of glycerine. The glycerine prevents drying out. In this medium the colors are retained, and the specimens remain opaque as is desired for observation by reflected light. A binocular dissecting microscope is best for observing preserved material. The insects, well-covered with fluid, should be placed in a Syracuse dish and are best seen against a white background. For detailed study low magnification with a compound microscope id desirable (A. R. Whiting, 1933a). A few specimens may be placed in a drop of glycerine on a slide covered with a small cover glass. Although the glycerine clears eventually, opacity will be retained long enough for careful study and drawing during a laboratory exercise. Reimmersion in alcohol will restore opacity, and the same specimens may be used several times. A pipette is useful for returning the alcohol to the vials, and the insects may be picked up with a camel's hair brush.

The rearing of Habrobracon as an experimental animal is dependent upon many factors, the most important of which is the culturing of its host, Ephestia kuhniella. These insects show a complete metamorphosis, and it is the larval stage that is utilized in rearing Habrobracon. The Ephestia larvae are about five-eighths of an inch in length when full grown. Success in rearing the moths is attained with rolled wheat (Pettijohn's Breakfast Food) or untreated yellow corn meal. These cereals appear to furnish

the optimum stimulation for oviposition, and the larvae feed well upon them and grow large and fat if ample floor space is provided in breeding boxes. The moths scatter their eggs over the cereal and these hatch in approximately a week, the time varying according to the temperature. The young larvae spin webs attaching particles of cereal together. After two or three weeks, an inspection should reveal webbiness of the cereal, denoting successful pairing and fertility. If temperature is high the larvae will attain full size in four weeks from time of isolating the parental moths. A warm temperature 27-30° C. gives best results, but humidity must be fairly high, 80-90 per cent, or the young larvae will not develop. Pupae are formed in silken cocoons. The entire period from egg to eclosion may be reduced to five weeks, but usually six weeks are required for a generation in summer weather. Eclosion begins at the end of this time, and moths will continue to emerge for three or four weeks or longer.

Moths rest on the cover, sides of box, or on the cereal, and may be conveniently collected in a shell vial. A vial is placed over each one, and at the same time the culture box or cover is tipped in such a way that the insect will fall down into the vial when touched by it. If many moths have emerged and are inconveniently active, the box may be cooled slightly to quiet them. Several individuals, approximately twenty, are collected in the vial which is then inverted into new culture medium. The development of Ephestia larvae may be arrested for prolonged use by placing the culture in a cold place.

Chapter IV

GENE MUTATIONS

Habrobracon juglandis has proved to be excellent material for the study of gene mutations which produce visible effects, since the haploid nature of the males prevents recessives from being carried over more than one generation before the mutant individuals appear. Most mutations occurring in the germ tract of a normal wild-type female will appear in her mutant sons if her eggs are not fertilized. Should her mutant eggs be fertilized, her daughters that develop from these eggs will produce sons, fifty per cent of which will show the new trait. Recessive mutations occurring in the germ tract of a normal wild-type male will become evident in certain of his grandsons; that is, in half the sons of those daughters which developed from eggs fertilized by sperm bearing the mutant gene. Of course, this ratio may be disturbed by the lowered viability of the mutant. Several mutations have occurred spontaneously in wild-type stocks. These have involved eye color, shape, and size; body color, shape, and size; wing pattern, shape, size, venation, and position; antennal length, structure, and position; leg length and structure; foot structure; varying degrees of lethality; and sex. Muta-

tions have also been induced through X-radiation and temperature variation.

Variations in eye color were among the first mutations to be observed. A quadruple allelic series of factors affecting eye color was reported (A. R. Whiting and Burton, 1926).

ORANGE, o (eyes). The normal wild-type, jet black eyes and dark brown ocelli, mutated to orange, in which the ocelli have but a slight trace of pigment while the eyes are orange varying to pink and red. The first appearance of orange (P. W. Whiting, 1921c) was in a single male found March 27, 1920. Crosses between orange and wild-type gave the first definite genetic check on the supposition that males, being haploid and from unfertilized eggs, inherit only from the mother. They also gave the first indication that related parents occasionally produce a few sons from fertilized eggs which are diploid and like their sisters in appearance.

IVORY, o^i (eyes). On June 24, 1924, there appeared in a fraternity of orange stock, four ivory-eyed males. Ivory has colorless ocelli and compound eyes of a greenish white with occasionally a trace of pink. This mutation has proved to be recessive to both wild-type and to orange, forming the third in an allelic series.

LIGHT-OCELLI, o^l (eyes). In January, 1925, there appeared from a cross of ivory female by wild-type male a single female with light ocelli but with the compound eyes black as in wild-type. This mutant proved to be an allele of

ivory, and hence the mutation took place in
spermatogenesis involving at least one sperm.
Light-ocelli has black eyes but ocelli are very
light in compound with ivory or with orange.
In pure light stock the ocelli may be charac-
terized as light brown, somewhat darker in the
males. It was found to be recessive to type
and, as regards compound eyes, dominant to
orange and to ivory. In combination with orange
or ivory the ocelli were lighter than in the
homozygous condition. Light-ocelli was lost
before the appearance of a fifth allele, dahlia,
and, therefore, was never tested with that or
with any eye colors found later.

DAHLIA, o^d (eyes). The fifth allele in the
orange locus appeared December 1, 1929, from a
cross of an ivory female by a wild-type male.
A single female with light ocelli and eyes very
dark reddish-brown appeared. This mutant, called
dahlia, proved to be dominant to orange and to
ivory although somewhat lightened in combina-
tion with either. In view of decreasing domi-
nance associated with decreasing pigmentation
in this series, it is probable that light-ocelli
would have come between wild-type and dahlia,
could it have been tested.

The locus, orange, appears to be especially
unstable, but there is certainly no striking
increase of mutability correlated with X-ray
treatment (P. W. Whiting, 1932a). P. W. Whiting
(1928b) reported a very high correlation be-
tween mosaicism and apparent mutation for this
locus. The orange series is female fertile
with good viability of both males and females.
These stocks, except for light-ocelli, are be-

ing carried in the homozygous state in the laboratory for genetic studies.

CANTALOUP, c (eyes). The first eye mutation not in the orange locus was cantaloup, recessive to wild-type. A female from orange stock was treated by P. W. Whiting in March, 1928, with X-rays (dosage about 1100 R units). One male with eyes resembling ivory was produced, and subsequent tests proved it to be a new mutation. At the time of emergence cantaloup eyes appear white with a slight greenish tinge. They quickly change to a light pink and frequently darken so as to resemble orange or carrot, which will be described later. After death they usually become black, differing in this respect from orange and carrot, which show no corresponding change in color. Ocelli are colorless. No other allele has been found at this locus. In a mixed culture it may be confused with ivory or with orange. Both males and females are fertile, and this type may be kept in a homozygous condition.

MAROON, ma (eyes). Another locus has become marked by maroon, a form resembling dahlia. This mutant was found in January, 1931. Maroon has light ocelli with the compound eyes a very dark red, so dark that it is often necessary to use the light ocelli as an aid in separating it from wild-type. This stock is male and female fertile and can be kept homozygous.

WHITE, wh (eyes). Another allelic series involves white and carrot. White first appeared in June, 1931, and resembles ivory in color

with colorless ocelli. White is of normal viability and fertility. In combination with shot-veins, to be described later, white consistently shows small red flecks scattered in the posterior and ventral part of the eyes. White shot-veins is, therefore, known as variegated (Fig. 3).

CARROT, wh^3 (eyes). In March, 1932, mutant males with carrot eyes appeared. This eye color closely resembles orange. White is almost dominant to carrot. The white-carrot heterozygote has a yellowish cast by which it can be accurately separated from white. Both of these alleles are of normal viability and fertility.

SPECKLED, Sk (eyes). This factor is due to a dominant gene and results in numerous small, bright red flecks of pigment in a white eye. Preliminary work indicates that the specks are not on the cornea but lie in the soft tissue beneath. They do not appear in the pupal eye until about the third day of pupal life. Speckled varies in its expression in the two sexes and is sensitive to temperature. At 30° C., a few specks are visible in the eyes of the females, which vary among themselves in the degree of speckling. At room temperature, specks are usually lacking in female eyes. In males at 30° C., the degree of speckling is very pronounced both as to depth of coloration and number of specks. Although specks are scattered at random throughout the compound eye, there is a denser speckling in the ventral half of the eye. Males, too, vary among themselves in the intensity and the number of specks. At room
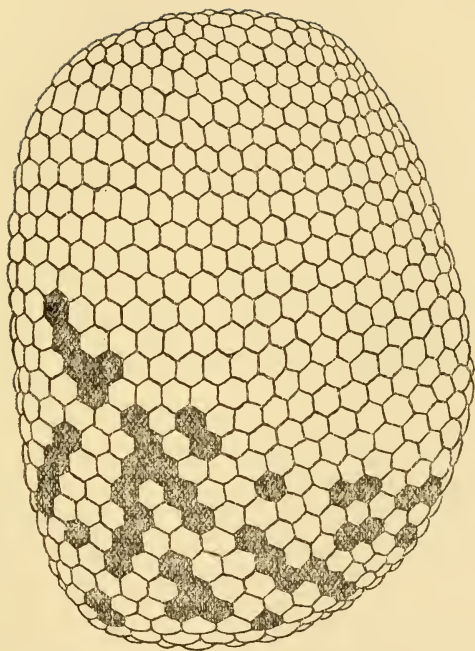
Fig. 3. Right compound eye showing effect of the mutant, shot-veins, in a white eye. The darkened areas are red in the living animal.   X   160

temperature, if the lighting is good, a few specks can usually be distinguished in males. So far, white is the only underlying eye color that will differentiate speckled. This mutant is of normal viability and fertility.

RED, rd (eyes). Red is a recessive factor for eye color which is not allelic to orange. It varies considerably in intensity, depending on the temperature, from a light red to a dark red almost black. The ocelli are a light pink and can be used as an aid for distinguishing the very dark red eyes from wild-type. This mutant is female fertile, and the males are of normal viability.

PELLUCID, pl (eyes). Pellucid is an eye mutant in which the compound eyes are semitransparent. It is female fertile, and the males are of normal viability.

PINK, pk (eyes). This is an eye mutation in which the compound eyes are pink. It appeared in the progeny of an X-rayed female in the summer of 1945. It is of normal viability and fertility. (Discarded)

TINTED, tn (eyes). This mutation can best be observed in combination with white. In this combination the compound eyes are not opaque but have a grayish cast with a semitransparent background. It is female fertile, and the males are of normal viability.

MOTTLED, mo (eyes). This is an eye mutation in which the compound eyes are not uniformly black

but have purple splotches in the ventral portion, and the ocelli are light. It is female fertile, and the males are of normal viability.

GLASS, gl (eyes, antennae, and tarsi). In October, 1931, mutants having smaller eyes and slenderer antennae than normal were found in a fraternity from a female heterozygous for orange and maroon. Glass eyes lack facet outlines and resemble the shiny, immature eyes of developing pupae. Sections of glass eyes show incomplete tissue differentiation; hence, this mutation may result in arrested development of the eye. Ocelli apparently are not affected. Antennae are very slender and of uniform diameter. The tibial spurs of the prothoracic legs are small while those of the mesothoracic and metathoracic legs are lacking. The foot is much malformed and reduced in size with claws very small or lacking. Glass females are weak and of decreased fertility. Glass males are of good viability.

GLAZE, gz (eyes). This mutant appeared in the summer of 1934 in the offspring of an X-rayed female (dosage about 4000 R units). Glaze resembles glass, but antennae and tarsi are not affected. It is female fertile with males of normal viability.

SHINY, gz^S (eyes). Shiny is an eye mutation where the compound eyes are of the wild-type black but show a very enamel-like gloss on their surface. In various tests it has been found to be allelic to glaze. Both sexes are fertile with normal viability. (Discarded)

TRANSPARENT, tp (eyes). This is an eye muta-
tion in which the compound eyes have a trans-
parent appearance. It shows up only with light
eye colors. It is female fertile, and the males
are of normal viability. Several recurrences
of this mutation occurred in the summer of 1945.

LIGHT-OCELLI, lo (eyes). This mutant appeared
in the summer of 1934 in the offspring of an
X-rayed female (dosage about 5000 R units).
Here normal wild-type black compound eyes are
accompanied by light ocelli. This mutant was
not allelic with orange, and both sexes were
found to be fertile. (Discarded)

PORT, pt (eyes). This mutant appeared in the
summer of 1934 in the offspring of an X-rayed
female (dosage about 4500 R units). Here com-
pound eyes are of a dark red color with light
ocelli. In this mutant the males appeared to
be sterile, and it was lost immediately after
appearance.
    The several cases of eye-color "mimics" are
of some interest. White and ivory are indis-
tinguishable except under a high magnification,
when it can be observed that white is more
translucent than ivory. Both have a slight
greenish tinge. Carrot is somewhat more pink
than orange although very similar to it, while
dahlia and maroon resemble each other with dah-
lia tending on the average to be lighter. Any
two of these "mimics" crossed together recon-
stitute the dominant in the Fl females.
    Multiple recessives are as light as or
lighter than any single mutant type entering
into their genetic constitution. In the major-

ity of cases they lack pigment. Dahlia and maroon form a double recessive which is but slightly different from either single type. The lightening influence of one mutant on another is not necessarily correlated with intensity of its color. For example, maroon is darker than dahlia, but when combined with carrot it gives white, whereas dahlia-carrot is a somewhat lightened carrot (A. R. Whiting, 1934).

Mutations for eye size and shape have not been as numerous as have those for eye color.

KIDNEY, k (eyes). A mutation to kidney eye shape was found on August 18, 1930, and was described by P. W. Whiting (1932a). The mutant appeared in a male with compound eyes lacking with the exception of a very minute one on the right side. Ocelli were of approximately normal size. The mother had been X-rayed with a dosage of 2600 R units. When the wasps are bred at 30° C., compound eyes and ocelli are reduced in size and elongated dorso-ventrally, some of them kidney shaped. The majority of specimens are inviable, many dying in cocoons as elongate pupae often with small heads. At lower temperature, 25° C., for example, they are of excellent viability and both sexes are fertile.

W. F. Dunning (1931) obtained two mutant types, "small" and its allele "extreme small." These have proved allelic with kidney.

SMALL-EYES, k^s (eyes), and EXTREME-SMALL, k^e (eyes). These alleles are of normal viability and fertility. A study has been made of dominance in the kidney-extreme-small compound fe-

males as affected by temperature differences
(Speicher, 1932b, 1933a,b, 1934a,b). The eye
size of mutant-type wasps showing this charac-
ter is extremely variable, ranging from a total
lack of eyes to those which, though approaching,
never reach the normal size (Fig. 4). The in-
dividual facets, when present, are of normal
shape and size, the variation occurring as a
decrease in the total number. The sizes of
right and left eyes vary somewhat independently
of each other. The ocelli are likewise affected
and are also extremely variable, ranging from
none at all to those apparently normal in size.
Although no actual measurements have been made,
it has been noted that the ocelli of any one
individual tend to be of the same size. Aside
from the modification of compound and simple
eyes no other external effect is manifest.
(Discarded)

SMALL, sm (eyes). This mutant appeared in the
summer of 1934 in the offspring of an X-rayed
female (dosage about 4500 R units). This mu-
tant, in which the compound eyes are much re-
duced in size, closely resembles small-eyes.
It was discarded soon after its appearance.

EYELESS, el (eyes). W. F. Dunning (1931) re-
ported a mutation which she called eyeless, a
recessive mutant type in which the heads are
much malformed when the wasps are bred at 30° C.
with large lobes on either side. At lower tem-
peratures these lobes fail to appear. Rudi-
ments of compound eyes may be present, and the
wings tend to be somewhat wrinkled. Both sexes
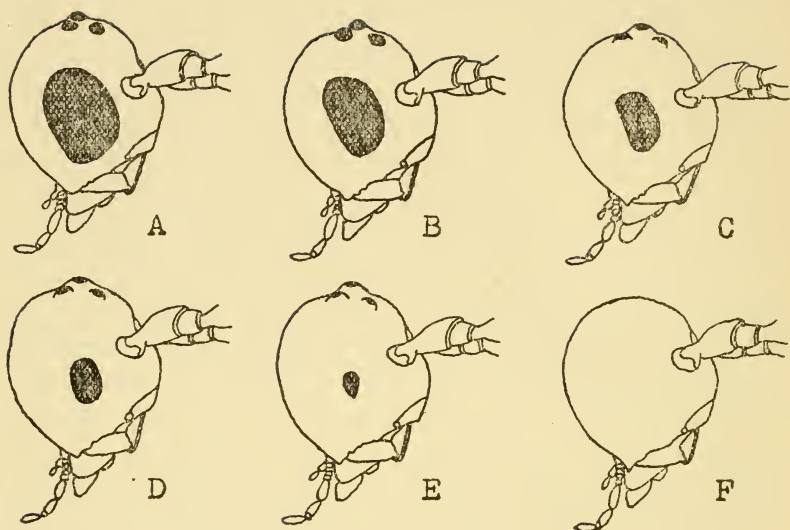are fertile, but females are somewhat weak.

Fig. 4. Eyes of wild-type (A) and
mutant type (B - F) wasps. From a
study of the kidney-extreme-small
alleles. B. R. Speicher, 1932b.

Viability of males is about fifty per cent that of their wild-type sibs. (Discarded)

BAR-EYES, be (eyes). W. F. Dunning (1931) reported on another eye mutation, which she called bar-eyes, a recessive mutant type. Males are fertile, but 121 tested females proved sterile. (Discarded)

CRESCENT, cr (eyes). In August, 1931, an eye mutation affecting both ocelli and compound eyes appeared in a fraternity of 35 males. The compound eyes are slightly smaller than normal, and the ocelli are crescent-shaped. Crescent is of normal viability and fertility in the male, but fertility seems slightly reduced in females.

PEBBLED, pb (eyes). In March, 1932, five males of a fraternity had a new eye character, pebbled, with facets irregularly arranged and eyes somewhat smaller than normal. Pebbled males are rather small and they mate with difficulty. The females are weak or sterile. Viability of males is normal. (Discarded)

BULGE, bu (eyes). In this mutant type the compound eyes are abnormally bulged transversely. Both sexes are fully fertile with normal viability.

Mutations for body color have not been as numerous as have those for eye color. The wild-type individuals vary in color from honey-yellow to almost black, depending upon the temperature at which they are reared; the higher the temperature, the lighter the color. During

the time in which Habrobracon has been reared in the laboratory, six mutations in body color have come to light. Three of these mutants, black, honey, and lemon, are fully fertile and can be kept as homozygous stocks with each color separate or in any desired combination. The remaining three mutants, cheese, silver, and sooty, have been discarded. Breeding tests have shown that the genes for the first three mutant body colors are linked and are, therefore, on the same chromosome.

BLACK, bl (body). The recessive mutant black was found among descendants of X-rayed material. Later a recurrence of the same gene appeared among the progeny of another X-rayed mated female (A. R. Whiting, 1939b). The factor blackens the animal to an extreme degree, even at higher temperatures. The black pattern is similar to that of wild-type reared at 21-22° C., but yellow areas are considerably lighter, almost cream in fact. The stemmaticum remains very black while the praescutum differs from that of wild-type at a lower temperature in the shadowy continuation of the median patch to the posterior edge. Dissection shows this pattern to be entirely within the cuticle. Legs are completely black and wings and antennae darkened. The whole animal presents a glistening jet-like appearance which becomes even more striking at 19° C. Dissection reveals in the praescutum a ghost pattern corresponding to the light areas of higher temperatures, but no trace of the light spots characteristic of the mesoscutellum. Mandibular teeth are black. No difficulties are encountered in

separating black from wild-type whatever the conditions of rearing, for the final check is always extent and intensity of yellow regions on head and legs. They remain more extensive and a deeper yellow in wild-type.

HONEY, ho (body). In 1932 a type female produced eight daughters and six sons. One of these males lacked black pigment entirely. This trait was found to be hereditary and recessive, and it was called honey. Black pigment is everywhere absent, even in animals reared at low temperatures. A praescutal pattern similar to wild-type may be observed, but this is represented in darker yellow or red instead of black. This pattern is in the cuticle and not in the structures beneath it. At 30° C., honey has the same color as wild-type raised at a temperature high enough to prevent the formation of black in the body. This trait is associated with good viability, but females are of reduced fertility.

LEMON, le (body). In September, 1933, one male with lemon body color appeared in a fraternity of 124 males bred from a virgin female (P. W. Whiting, 1934b). A wild-type female had been crossed with a gynoid (to be described later) male which had been X-rayed (dosage about 3500 R units). The trait is very striking, the ground color being pale lemon-yellow, rather than honey-yellow as in wild-type and honey. The black pigmentation of the feet, female gonapophyses, and wings appears perfectly normal while the antennae are black except for the two basal segments which are lemon-yellow.

Lemon thus shows a striking contrast to honey, and is partially dominant to wild-type. Pale basal segments and characteristic lemon praescutal pattern are dominant whereas general body color of the heterozygote resembles wild-type. There are present on the praescutum two distinct anterior bands sharply divided by a light line, and below these, irregular spots, often asymmetrical. Study of the cuticle of the lemon thorax by means of sections and removal from tissue underneath shows that the black pattern is in the cuticle itself. The spotted effect results from internal structures showing through the transparent portions which correspond to the yellow regions in the wild-type and other mutant forms. The two praescutal bands, characteristic of lemon, outline more accurately the muscle masses beneath than does the solid patch of non-lemon forms, for dissection reveals a definite longitudinal division in the muscle masses of this region in all color types. This dividing line in the praescutal pattern is mentioned by Schlottke (1926) as appearing in some wild-type individuals at high temperature, and it sometimes shows in honey as a darker line in the center of the median praescutal patch. In lemon, however, it is consistently present and more extreme. Lower temperatures change the black pigment of the lemon mutant less strikingly than that of wild-type or black. The black areas never become as intense or widespread, but in spite of this there is a striking lightening of yellow. The females of this mutant are fully fertile, and the males are of normal viability (A. R. Whiting, 1939b).

CHEESE, ch (body). This mutant appeared in the summer of 1934 in the offspring of an X-rayed female (dosage about 4500 R units) (P. W. Whiting, 1935b). Cheese is a pale, opaque, greenish-yellow, and the color is especially noticeable in the head. It was discarded soon after its occurrence.

SILVER, si (body). This mutant appeared in the summer of 1934 in the offspring of an X-rayed female (dosage about 4500 R units). In this mutant type pigmentation is apparently arrested since the body fails to darken. This mutant has been discarded.

Variation in general body pigmentation is controlled largely by temperature, but influence of hereditary factors is also obvious. When reared at 30° C., the wasps show differences in color of the mesosternum.

SOOTY, s (mesosternum). A factor for sooty mesosternum was shown (P. W. Whiting, 1926a) to be linked with defective (see wing mutations). This mutant has been discarded.

A few mutations affecting body size and shape have occurred.

MINIATURE, m (body). One mutation for body size occurred in March, 1928. Six sons from a female mated to an X-rayed male (dosage about 2950 R units) appeared with body size much reduced. The primary wing is less rounded on the costal margin. The antennae are shortened, both by shortening of the segments and by reduction of their number. There is also some irregularity in the way the segments are set

together. No marked disproportion appears in the reduction of the size of the legs. Miniature is a semilethal. Many die as pupae. Adult males are of good fertility, but adult females are almost sterile. (Discarded)

BROAD, br (thorax). In August, 1930, a number of males were found with thorax abnormally broadened. There is some tendency toward reduplication in the wings. The mutant type was first noticed in about 50 per cent of the sons of two different sisters. The character is somewhat irregular, and it cannot be stated with certainty that this represents the first appearance of the mutation (P. W. Whiting, 1932a). Broad may be called an irregular recessive, but about 50 per cent of the heterozygous females show the trait to a slight extent. Broad has good fertility and viability. (Discarded)

SMALL-HEAD, sh (head). This appeared in the progeny of a mated female that had been X-rayed (P. W. Whiting, 1929b). Wasps exhibiting this mutation have very small heads. The mutant type is much more distinct in the homozygous females and shows considerable overlapping in the males. It is of good fertility and viability. (Discarded)

EXTENDED-HEAD, Eh (prothorax). In July, 1931, an X-rayed mated wild-type female (dosage about 3840 R units) produced in her progeny one male with an extended head, which proved to be a dominant mutation (N. C. Bostian, 1931). In this mutant type, the membrane dorsal to the

prosternum is much expanded so that the head is
thrust forward. When dead and dried, the mu-
tant type cannot be distinguished from normal.
Heterozygous females have fertility somewhat
reduced. Extended-head males have their via-
bility reduced somewhat less than fifty per
cent as compared with their wild-type sibs.
(Discarded)

By far the most numerous mutations in Habro-
bracon, are those affecting the wings. Shape,
size, position, and venation may be affected
singly or in combination. The normal wild-type
wing is fairly regular in outline with a few
definite veins (Fig. 5). The wing mutations,
like all others, have been named from the ef-
fect most obvious to the discoverer.

DEFECTIVE, d (veins). Defective is one of the
most common of the wing variations occurring in
nature. This mutation involves a break in the
fourth branch of the radius vein (R4). Multi-
ple genetic factors are involved, and tempera-
ture influences the trait, the greater defect
being correlated with higher temperature (P. W.
Whiting, 1932a). A single gene occurring early
in breeding experiments, possibly derived from
wild-type stock (P. W. Whiting, 1924b), was
isolated and found to give about 95 per cent
phenotypically defective under standard condi-
tions, 30° C. Defective is of normal viability
and fertility. (Discarded)

WRINKLED, w (wings). Wrinkled occurred in a
female, and is the result of a mutant factor
causing difficulty in shedding pupal integument
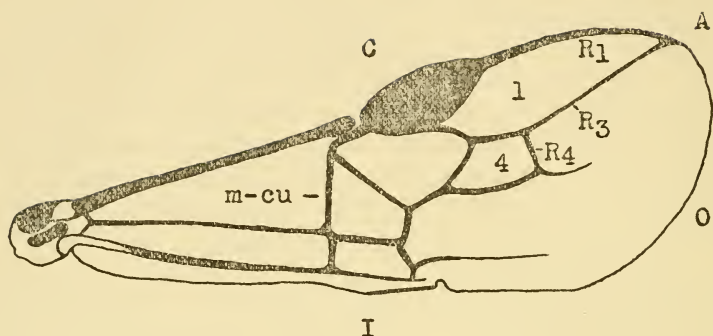(P. W. Whiting, 1926b). As a consequence ir-

Fig. 5 . Right primary wing. C. Costal margin.
O. Outer margin.   I. Inner margin.   A. Apex.
R_1, R_3, R_4. First, third and fourth branches of
radius vein.   m-cu. Medio-cubital cross-vein.
1, 4. First and fourth radial cells.
P. W. Whiting, 1932c.

X 47.

regular wrinkling of the wings results, and portions of the integument are found adhering to the antennae which show a tendency to fragment. Wrinkled is fertile in both sexes but is mechanically hampered in eclosion and in other activities. (Discarded).

REDUCED, r (wing size). This mutation occurred in March, 1925 (P. W. Whiting, 1926b) in a single male which had small wings and irregular reduced venation (Fig. 7). The trait is variable but always distinct from type. Reduced affects chiefly the middle area of the wings and usually causes disappearance of vein m-cu. It is of good viability and fertility in both sexes.

SHORT, sh (wings). This mutation was first observed in cultures derived from some of the sibs of the miniature mutants (P. W. Whiting, 1932a). It is uncertain whether short occurred as a mutation at approximately the time of the mutation to miniature or whether it had been carried in the stock. Short is very susceptible to temperature, overlapping with normal to a considerable extent. It is impossible to distinguish a culture of short from type when reared at room temperature. Under standard conditions, 30° C., wings of short average much smaller, but even in this case there is more or less overlapping. Females are fully fertile, and males are of normal viability. (Discarded)

NARROW, n (wings). Narrow was first observed in April, 1930. Fourteen males appeared from a cross between a type female and a type male

that had been X-rayed (dosage about 2100 R units). Narrow cuts off irregular slices of both wings on costal and inner margins. It is somewhat variable but does not overlap with type. It is of good viability and fertility in the male, but females are apparently sterile. (Discarded)

WAVY, wa (wings). Wavy appeared in June, 1930, from a wild-type female that had been mated to an X-rayed wild-type male (dosage about 2740 R units). Wings of wavy are shortened, showing transverse waves which are especially noticeable near the distal part of the costal margin. Antennae are usually normal, but in many cases one or both become markedly depigmented distally, the segments tending to drop off. Fertility and viability of males are good, but females are somewhat weak.

VESTIGIAL, v (wings). Vestigial is a wing mutation found in August, 1930. A virgin mother produced a number of vestigial winged males. Vestigial is semilethal, many wasps dying before eclosion. Fertility in the males that eclose is good, and many of them live a normal length of time. (Discarded)

SPREAD, sp (wings). This mutation appeared in May, 1930, from a male fraternity of orange stock. Eight males with wings spread out to the sides were observed. Further examination showed that these males had light areas on the mesopleura in the position of insertion of the directive wing muscles. The wings themselves are normal, and the defect is probably muscu-

lar. The trait grades into type. It was im-
possible to obtain offspring from female spread.
Males are of normal fertility. (Discarded)

NOTCH, No (wings). Notch is a mutation affect-
ing the outline of the wing. It appeared in
April, 1930, in the progeny of a type female by
a tapering male (see antennal mutations). Notch
exerts its effect on the margin of either pri-
mary or secondary wings; the notches may be
terminal or lateral. The first branch of the
radius vein is shortened, causing the usual
rounded lobe of the wing to be notched; how-
ever, there is much irregularity and asymmetry
in the expression of this factor. Notch does
not breed true, and it is very likely that there
are more factors than one involved. In many
cases the trait acts like a dominant lethal.
(Discarded)

SHOT-VEINS, sv (veins). Shot-veins is a semi-
dominant factor that arose simultaneously in
three different lines after extreme heat treat-
ment of larvae. It causes veins of the wings)
to be broken and distorted (Fig. 7). This mu-
tant was found in August, 1930. Shot-vein stock
has proved to be fully fertile and stable. In
connection with studies of linkage made in
1931, shot-veins was crossed to white eyes, and
the Fl females bred as virgins. The double re-
cessive, shot-veins and white eyes, showed a
mottling of red spots in the posterior ventral
region of the compound eye. It has since been
observed from very large numbers that these
spots are present in both eyes of all white-
eyed individuals with shot-veins. Their dis-

tribution and intensity show some variation, but they can never be seen from the dorsal view. A homozygous, white shot-veins stock was derived and called variegated. This variegated stock has been found to breed true and to be of normal viability and fertility (A. R. Whiting, 1933f, 1934).

BENT-WINGS, bw (wings). In June, 1932, a virgin female produced a fraternity of eighteen males, five of which had bent-wings. In this mutation the wings are quite narrow and are bent anteriorly along the costal margin. The females are apparently unable to sting active caterpillars. However, when placed with paralyzed caterpillars a few may sting, feed, and lay eggs, but the eggs fail to hatch. The males are of normal viability. (Discarded)

GABLED, gb (wings). In March, 1932, an orange defective female (which had been mated with an X-rayed male) produced wild-type females. Seven of the azygous males obtained from them had wings which sloped when folded like gables of a roof. The mutant type is thus easily recognized in the vials. The wings have venation more reduced than in any other mutant type except veinless. The factor causes very poor viability; gabled males are less than ten per cent as frequent as their normal wild-type sibs from heterozygous mothers. Gabled females have not been produced (P. W. Whiting, 1934b). (Discarded)

FLARE, fl (wings). In February, 1932, a wild-type virgin female produced eleven males two of

which had wings in which the costal margin
flared forward distally. Flare overlaps with
wild-type so that classification is uncertain.
Flare females produce among their offspring
some which are phenotypically normal. Both
sexes are fertile and of normal viability.
(Discarded)

INDENTED, in (wings). In December, 1931, an
orange defective female, X-rayed (dosage about
1500 R units) as a five-day larva, was subse-
quently mated to a wild-type male. An F1 fe-
male produced eighteen males of which five had
the primary wings somewhat indented toward the
tip. Indented frequently shows irregular thin-
ning of the radius veins beyond the stigma in
primaries and irregular narrowing of the secon-
daries. Viability is normal and females are
fertile. (Discarded)

CUT, ct (wings). In February, 1931, six azy-
gous males with cut wings appeared in a frater-
nity. The outer margin of the wing is greatly
indented or straightened giving a cut appear-
ance (Fig. 6). The trait is very variable but
may be readily recognized. Viability and fer-
tility are normal.

STRAP, sr (wings). In January, 1932, three males
with strap wings appeared in wild-type stock.
The first and third radius veins are greatly
shortened and the outer margin of the wing is,
therefore, given a lobed appearance. The trait
is very pronounced and of equal viability with
wild-type. (Discarded)

CONFLUENT, cf (wings). This is a mutation affecting wing veins and antennal segments. It was found on August 2, 1930, in a male with shortened wings showing fusion between first and third branches of radius veins at their extremities. There is more or less fusion and deficiency of segments distally in the antennae. Degree of abnormality in wings is correlated with that of antennae. At slightly increased temperature many confluents die in cocoons, and at lower temperature confluent overlaps with wild-type. Females are fully fertile and males are of normal viability. (Discarded)

TRUNCATE, tr (wings). This mutation was found on August 7, 1930, in the offspring of an X-rayed female (dosage about 2600 R units). One of the male progeny had primary wings much shortened distally tending to cause coalescence of the first and third radius veins. Truncate is very irregular in appearance, apparently having a considerable overlap into type. Terminal antennal segments are very likely to be more or less fused, and wings are often but slightly affected. The variation suggests confluent in certain respects, but in combination with reduced it is more easily recognized. Both sexes are fertile with normal viability. (Discarded)

UNEXPANDED, un (wings). This first appeared in the progeny of a type female by a wild-type male in August, 1930. Wasps with this mutant trait have primary and secondary wings unexpanded. This character was carried for several generations, but the wasps were highly invia-

ble, the majority dying in cocoons. Females were obtained, but were inviable and the stock was discarded.

POINTED, p (wings). In July, 1931, N. C. Bostian (1931) X-rayed (dosage about 3200 R units) a wild-type mated female. One of the daughters produced among her progeny twelve males with pointed wings. The tips of the wings of this mutant type, both primaries and secondaries, are narrowed and wrinkled, the narrowing being especially noticeable in the radial cell. Females are sterile: they sting caterpillars, feed and lay eggs, living for several days, but the eggs fail to hatch. Pointed males appear in normal numbers from heterozygous mothers. (Discarded)

TRUNCATED, td (wings). In December, 1931, an orange defective female, X-rayed (dosage about 2000 R units) as a five-day larva, was subsequently mated to a wild-type male. An Fl female produced among her progeny five males with truncated wings. The first radial cell in the primary wings of this mutant type is greatly reduced, the wing is narrowed slightly, and the outer margin assumes a squared appearance. The trait is variable but easily recognized and does not overlap with wild-type as does truncate, previously described (P. W. Whiting, 1932a). Truncated females are weak, failing to sting caterpillars or to oviposit. Truncated males appear in normal numbers from heterozygous mothers. (Discarded)

SMALL-WINGS, sw (wings). In March, 1933, six males appeared showing a mutant trait, small-wings. These were among the progeny of an Fl female from a cross between a heterozygous orange female by a narrow winged male. In this mutant type venation appears perfectly normal but wing size is greatly reduced, and there is no overlapping with wild-type (Fig. 6). Small-wings is of good fertility and viability.

CREPE-WINGS, cw (wings). In April, 1932, a heterozygous female produced a fraternity of seven males including two with wings irregularly wrinkled. The outer margin of the primary and secondary wings is very irregular, and the surface of the wings resembles crepe paper. The trait is variable but easily recognized. The mutant type is somewhat over fifty per cent viable as compared with wild-type sibs. Females are of decreased fertility. (Discarded)

DROOPY, dr (wings). In March, 1933, a mutant type with wings held out and sloping downward appeared. Droopy males occur in good numbers but are likely to die in cocoons. They are less viable when reared at 23° C. than at 30° C. Droopy females try to sting the caterpillars but have produced no offspring except in one case when droopy males only appeared. (Discarded)

EXTENDED-WINGS, ew (wings). In July, 1932, five males with extended wings were found. This mutant type is easily distinguished when the wasps are active, but if they are etherized there seems to be no observable difference from wild-type. They must, therefore, be separated

in the active condition, which makes counting
tedious. The secondaries are extended lateral-
ly at an angle of 45 to 60 degrees from the
midline, and they also droop somewhat. Both
deviations from the normal are apparently the
result of deformation at the axilla. The pri-
maries may be held almost normally, or they may
be extended laterally at an angle approaching
or equal to that of the secondaries. The pri-
maries are not held downward like the seconda-
ries, but in the normal plane as though the ax-
illa of the primary is normal, and their posi-
tion is simply the result of a defect in the
secondaries. The abdomen is slightly elevated
as if for balance, especially in cases where
both pairs of wings are widely spread. The fe-
males are sterile but the males seem to be of
normal viability. (Discarded)

BROKEN, bk (wings). In 1934 a male with mutant
wings appeared in the progeny of an X-rayed
wild-type female (dosage about 4500 R units).
In this mutation the outer margin of the pri-
mary wings is broken and the wings are very
fragile. The veins in the primary wings often
resemble those of shot-veins. Broken and shot-
veins have been tested together and found to
segregate independently (Fig. 7). Both sexes
are fertile and of normal viability.

AEROPLANE, ae (wings and tarsi). This mutation
appeared in the progeny of an X-rayed female
(dosage about 3500 R units) in 1934. The wings
are stiffly outstretched, and the tarsi are
black and brittle. The males are unable to

mate, and the mutant was lost immediately after appearance.

EXTENDED, ex (wings). In 1934 in the progeny of a wild-type female, X-rayed (dosage about 4000 R units), a male appeared with wings held back but failing to fold over the body. This mutant does not show when the wasps are bred at room temperature. This mutant was not tested with others and was discarded soon after its appearance. This mutation recurred in the summer of 1945 in the progeny of an X-rayed wild-type female. Both sexes are fertile and of normal viability.

PINCHED, pd (wings). In 1934 this mutant appeared in a single male among the offspring of an X-rayed wild-type female (dosage about 4000 R units). The fourth radius vein is very short so that the longitudinal veins are drawn together giving the wing a pinched appearance. Both sexes are fully fertile and of normal viability. (Discarded)

REDUPLICATED, re (wings). In 1934 there appeared among the progeny of an X-rayed wild-type female (dosage about 4500 R units) a number of males with the primary wings more or less doubled. The mutant is variable, sometimes being indistinguishable from type. The males usually have drooping antennae, but the heterozygous females have normal antennae. This mutant seems to be semi-dominant since the heterozygous females usually have wings reduplicated. The females are fully fertile and the males are of normal viability. (Discarded)

ROUGH, ro (wings). This mutant appeared in the summer of 1934 in the progeny of a wild-type female that had been X-rayed (dosage about 3500 R units). In this mutant type the fourth radius vein is absent and the adjacent veins are roughened (Fig. 6). It is female fertile with males of normal viability.

VEINLESS, vl (wings). The veins of the wing are partially or wholly missing in this mutant, so that the major portion of the wing appears as an unbroken translucent structure. There is some variation in this mutant, but it is always distinguishable from wild-type (Fig. 7). Both sexes are fertile and of normal viability.

ELONGATE, eg (wings). In this mutant the first radial cell of the primary wings is elongated, and the outer margin of the wing is indented at the juncture of the third radius vein and the outer margin of the wing (Fig. 6). Both sexes are fully fertile and viable.

CRUMPLED, cp (wings). In this mutation the inner margin of the primary wings is not rigid and the entire wing surface is folded in a wave-like pattern giving the appearance of being crumpled (Fig. 6). The females are fully fertile, and the males are of normal viability. (Discarded)

CLIPPED, cd (wings). Here the primary wings are mere stubs with venation completely broken up. There is no wing pattern or variation in the mutant as the wing is so reduced that it completely obscures any classification of the
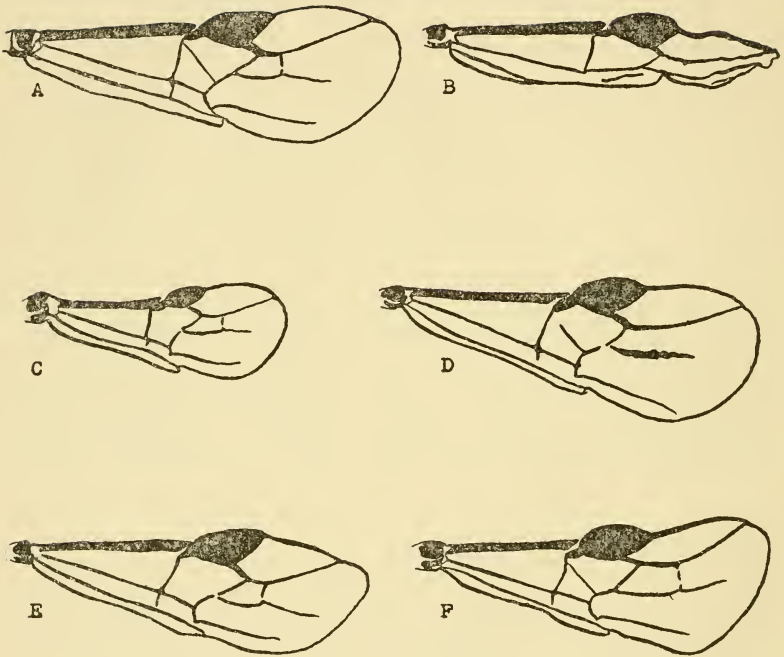
Fig. 6. Right primary wings of wild-type and certain
mutants. A. Wild-type. B. Crumpled. C. Small-wings.
D. Rough. E. Cut. F. Elongate.

X 22.
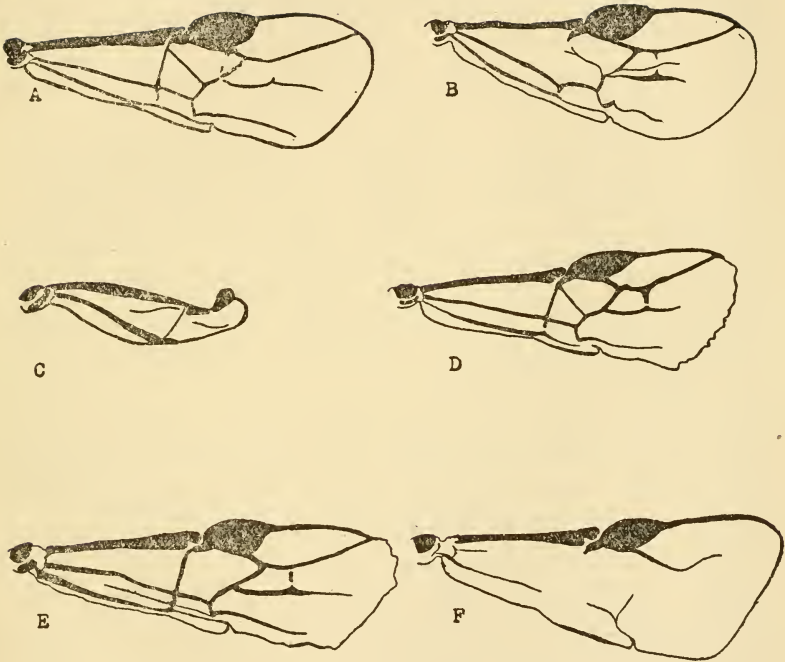
Fig. 7. Right primary wings of certain mutants. A.
Shot-veins. B. Reduced. C. Clipped. D. Broken. E.
Fused. F. Veinless.

X 22.

wings. The wasps are easily distinguishable. The clipped females are sterile and the mutant must be introduced through the males which are of normal viability (Fig. 7). (Discarded)

WET, wt (wings). This mutation occurred in the summer of 1945 in the progeny of an X-rayed female. In this mutation the microchaetae of the primary wings are irregular in length, giving the wings a wet appearance. The females are fully fertile, and the males are of normal viability.

Mutations for antennal length, structure, and carriage have occurred in Habrobracon. These factors may be found singly or in combination. Many of the genes cited in the present work cause greater or less tendency toward antennal deficiency; however, only those that show marked deviations in antennal form are listed as antennal mutants.

DEFICIENCY, de (antennae and posterior extremity). In this mutant type the antennal segments may be irregularly fused. Failure of normal development of structures at anterior or at posterior extremities sometimes occurs. External genitalia may be small or lacking, and the digestive tract may fail to open posteriorly. No definite factors have been isolated for these deficiencies; however, they have been shown to be partially controlled by heredity and to be highly correlated with age of mothers (P. W. Whiting, 1926c). (Discarded)

MINNESOTA YELLOW, My (base of antennae). In August, 1929, wild-type stock from Minneapolis,

Minnesota, included wasps with three or four
basal segments of antennae decidedly yellow
when reared at 30° C. The difference evidently
depends upon one gene with various modifiers,
determining the extent of the trait which may
be increased by selection. Minnesota yellow is
of normal viability and may be regarded as dom-
inant since heterozygous females show the trait
under standard conditions. (Discarded)

YELLOW, Y (base of antennae). In February, 1929,
two mutant males were found in the offspring of
a female that had been treated with X-rays
(dosage about 1460 R units) as a four day lar-
va. The mutants had the three basal segments
of the antennae strikingly yellow. The yellow
color is more definitely confined to the three
basal segments in this type than is the case in
Minnesota yellow, but lowering of temperature
during development induces melanogenesis in
both cases. Since heterozygous females show
the trait, it may be called dominant. Yellow
is fertile in both sexes but of lower viability
than wild-type. Distal segments of antennae
often appear pale and if temperature is but
slightly increased over standard, yellow wasps
become deformed and often die in cocoons. This
is not the case with Minnesota yellow in which
viability is normal (P. W. Whiting, 1932a).
(Discarded)

FUSED, fu (antennae and tarsi). A single male
was found in February, 1929, with antennal seg-
ments fused together and with tarsal segments
lacking or fused together (Fig. 8). The wing
of fused (Fig. 7) has a very characteristic and

constant indentation on the costal margin at
the apex. The female cannot reproduce because
of inability to feed from caterpillars. The
fused males, however, are fertile to varying
degrees, but they have some trouble in mating
because of the defective tarsi (Fig. 9). Fused
appears to be doubly effective in the duplex
state since fused diploid males have antennae
as short as those of the homozygous fused fe-
males; while in the haploid males with fused
antennae, the antennae are approximately the
same length as the antennae of normal females.
Two other occurrences of fused appeared in Feb-
ruary, 1931. These two recurrences of fused in
the same month are noteworthy as no fused was
being bred at the time. The two recurrences
were moreover entirely independent (P. W. Whit-
ing, 1932a).

LONG, 1 (antennae and wings). In June, 1929, a
number of males appeared with antennal segments
elongated and distal portion of wings shortened
and curved ventrally (Fig. 8). Segments of the
legs are somewhat longer and thinner than in
wild-type. Males with the mutant long are of
good viability and fertility but females are
rather weak.

SEMILONG, sl (antennae and wings). A wild-type
male was treated in June, 1930, with X-rays
(dosage about 2280 R units) and then mated to
three females. One of the daughters produced
in her progeny six mutant males which have been
called semilong because of their similarity to
long. Semilong males are of good fertility and
viability. Females are also viable and fertile

but rather weak. Antennal segments are length-
ened but are not as attenuated as are those of
long (Fig. 8). Leg segments are also somewhat
lengthened but heavier than corresponding seg-
ments of long. Distinction of semilong as of
long from wild-type is clear in antennae and to
a great extent in legs, but overlapping between
long and semilong apparently takes place espe-
cially in legs. The wing of semilong is quite
flat. Distal shortening, however, takes place
as is evidenced by the form of the outer margin
and especially by the abbreviation of the first
radial cell. A slight indentation is present
at the apex of the wing, not however, as pro-
nounced as in fused. It was first thought that
semilong might be allelic to long, but this
proves not to be the case.

TAPERING, ta (antennae). In May, 1930, nine
males with tapering antennae were found in a
wild-type culture. The antennae are very defi-
cient with much fusion and irregularity of seg-
ments distally (Fig. 8). Tapering does not
overlap with type, but reverse mutations have
occurred (P. W. Whiting, 1932a). Both sexes
are fully fertile and of normal viability.

ANTENNAPEDIA, ap (antennae). In the course of
genetic work involving tapering, wasps were ob-
served with tarsal-like claws on the terminal
segments of the antennae. A more or less well-
formed foot may be present (P. W. Whiting,
1934b). The distal segments may be modified to
resemble a tarsus with the terminal segment
provided with claws, arolium, and calcanea as
in the normal case. The foot may be present on

one or both antennae and is often imperfectly developed. The trait occurs in a large but variable proportion of the individuals of a selected strain. (Discarded)

LEGLIKE, lg (antennae). In April, 1933, males with leglike antennae were found in the progeny of a heterozygous female. Leglike is a much more extreme deviation than antennapedia. The entire antenna, except for the two basal segments, has been changed so that the grooves for the sensillae are absent and yellow color similar to that of the legs has replaced the black. Fusion of several segments distal to the two basal segments and swellings on the resulting mass suggest the malformed tibiae of certain types of inviable pupae (to be described later). The foot is provided with tarsal claws, arolium, and calcanea similar to a foot from the normal position. Leglike could not be reproduced because the males would not mate, and no sisters were produced. (Discarded)

ACIFORM, ac (antennae and female genitalia). In December, 1932, two sons of a wild-type female were observed to possess antennae with segments of the terminal half much reduced in diameter (Fig. 8). The mutant type males are of normal viability. Gonapophyses of females are much shortened, and the sting is usually defective; so that the females are sterile, failing to sting and feed on active caterpillars. The antennal character is easily distinguished, since the basal nine or ten segments are normal, but the terminal segments are much

narrower with more or less fusion and deletion
in both sexes.

DWINDLING, dw (antennae). In July, 1931, a mated
wild-type female was X-rayed (dosage about 3200
R units). Among her offspring was one male
with dwindling antennae. This mutant type shows
much irregularity and fusion of antennal seg-
ments in the male, but the proximal half of the
antenna is not affected. Females of dwindling
cannot be distinguished from wild-type pheno-
typically. Dwindling males are numerically
equal to somewhat over two-thirds of their nor-
mal brothers. (Discarded)

ATTENUATED, at (antennae and genitalia). In
May, 1932, a fraternity was bred consisting of
males, fifty per cent of which had antennae
with much malformation and fusion terminally.
Genitalia were also abnormal, and the type
could, therefore, not be perpetuated. The mu-
tation has been reported, and the mutant type
figured (P. W. Whiting, and A. R. Whiting, 1934).
The antennae are similar in appearance to those
of dwindling. (Discarded)

GYNOID, gy (antennae and abdominal sclerites).
In April, 1932, among the offspring of a het-
erozygous female, a male appeared having short
antennae resembling those of a female. This
mutant type, gynoid, the gene for which causes
haploid males to be weakly intersexual was
later described by P. W. Whiting, Greb, and
Speicher (1934). Gynoid males are similar to
normal males in internal structure and in ex-
ternal genitalia. Their ocelli are large re-

sembling those of normal males. Sclerotization of the abdomen is progressively heavier anteriorly, approximating the condition found in the female. Gynoid females are indistinguishable from wild-type. The trait acts as a recessive in heterozygous diploid males (P. W. Whiting, 1943b). This mutant is highly fertile and viable in both sexes.

SHORT, sh (antennae). In the summer of 1934, in the offspring of an X-rayed wild-type female (dosage about 4500 R units), a male was found with reduced antennal length. The mutant short resembles tapering, but the antennae are very much smaller. Both sexes are fertile and of normal viability. (Discarded)

STUBBY, sb (antennae). Males with antennae seven to nine segments long were observed in the offspring of an X-rayed wild-type female (dosage about 3500 R units). This mutant first appeared in the summer of 1934. The homozygous females for the mutant have antennae with five to seven segments. These few segments may be fused together giving the appearance of one or two large segments forming the antennae (Fig. 8). Both sexes are fertile with males of normal viability.

STUBBY-ABNORMAL, sb^a (antennae). Males with abnormally long stubby antennae were observed in a homozygous stubby stock. Breeding tests have shown that stubby and stubby-abnormal are allelic. Both males and females are fully fertile with normal viability.
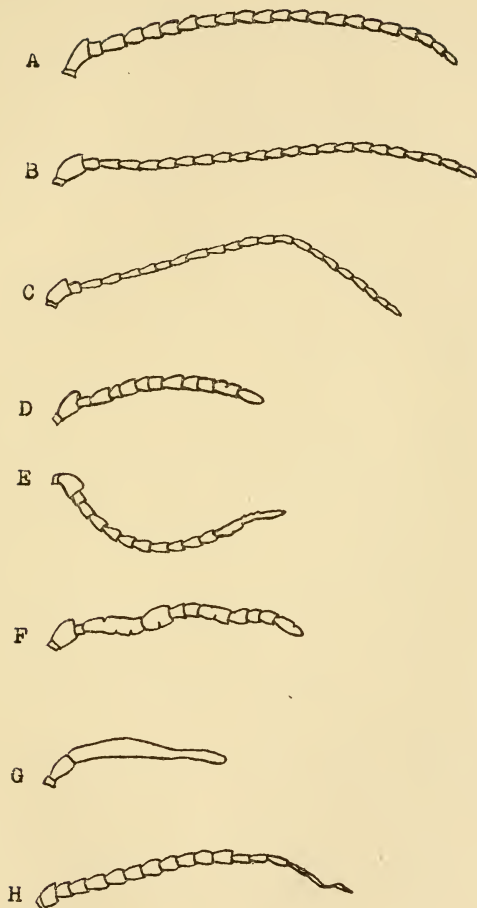
Fig. 8 . Right antennae of wild-type and certain
mutant type males.   A. Wild-type.   B. Long.   C.
Semilong. D. Stubby. E. Tapering. F. Coalescent.
G. Fused. H. Aciform.

X 24.

COALESCENT, co (antennae). In a fraternity of wild-type stock several males were observed with antennae of approximately normal length but with the segments coalescent. The females are fully fertile with males of normal viability.

A few mutations involving leg length and structure and foot structure have occurred in Habrobracon. These factors, like those for eye, wing, body, and antennal mutants, may be found singly or in combination. However, leg and foot mutants seem to cause reduced viability. This may be the result of a semilethal or their inability to mate properly.

BEADED, b (legs). In August, 1929, a fraternity of males was observed containing a number of mutants with beaded legs. The proportions of the various parts of the wing of beaded are very aberrant, and wings often fail to expand. Antennae are very likely to show fusion of segments and often more or less distal deficiency. Beaded is semi-lethal. The mutant types survive much better at 23° C. than at 30° C. Even at higher temperature the majority may attain the pupal stage, but few emerge from the cocoons. Tibiae and femora are much shortened and swollen, the swelling of the tibiae being confined to the distal half (P. W. Whiting, 1934b). Males of beaded are fertile, but viable females have not been found (P. W. Whiting, 1932a). (Discarded)

STUMPY, st (legs). In September, 1930, a single male with stumpy legs was found among the offspring of an X-rayed female (dosage about 3250 R units). The most striking characteris-

tic of stumpy is the extreme reduction of tar-
sal segments (Fig. 9). The appendages appear
otherwise normal. Stumpy may be called a re-
cessive, but a large proportion of heterozygous
females bear a spur at the tip of their protho-
racic metatarsi. More or less irregularity oc-
curs in tarsal segments of all legs so that
heterozygotes are not as sure footed as pure
wild-type. No metatarsal spur has ever been
found on middle or hind legs of heterozygotes
nor has a prothoracic metatarsal spur ever been
found in wild-type females. This spur closely
resembles the spur normally occurring at the
end of the prothoracic tibia. It may be pres-
ent on either or both front legs, but many het-
erozygotes fail to show it. Even in its ab-
sence it is usually possible to identify het-
erozygotes by tarsal irregularity. Stumpy is
of normal viability and fertility except that
females have difficulty in feeding from cater-
pillars and consequently may die without pro-
ducing eggs. Apparently they cannot brace them-
selves well enough to insert their stings for
puncturing in order to feed.

TWISTED, tw (legs). A male of wild-type stock
was X-rayed in January, 1930 (dosage about 3560
R units), and then mated to four females. In
the offspring of one of these females there ap-
peared fourteen males with twisted legs. Legs
of twisted show much malformation and irregular
bending. Many individuals fail to eclose, prob-
ably on account of mechanical difficulties. Males
are of normal fertility, but females are almost
sterile (P. W. Whiting, 1934b). (Discarded)
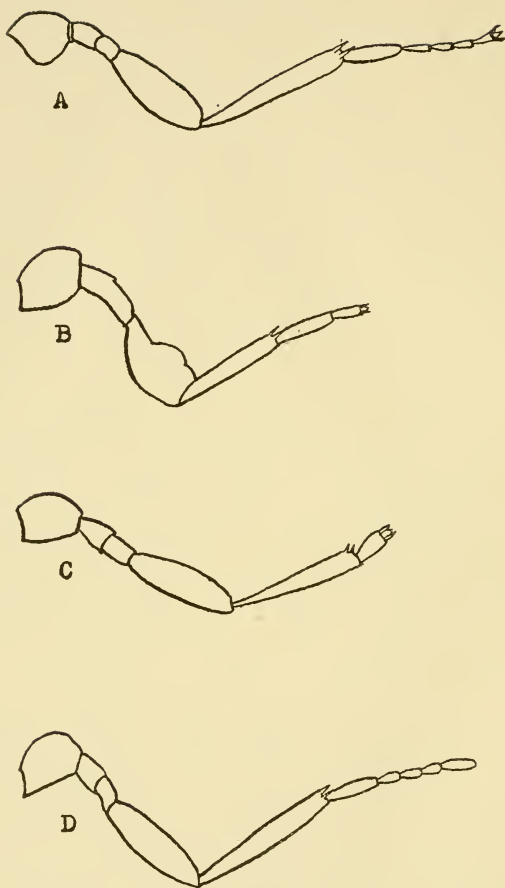
Fig. 9. Right metathoracic legs of wild-type and certain mutants. A. Wild-type. B. Fused. C. Stumpy. D. Footless.

X 26.

CONSTRICTED, Cs (femora). In August, 1930, a single female was observed with constricted femora. This mutant type is dominant and apparently lethal in the male. It is difficult to obtain offspring from constricted females, and fraternities are small. The difficulty is probably mechanical and concerned with feeding from the caterpillars. The trait appears in all three pairs of legs but is most obvious in the metathoracic pair (P. W. Whiting, 1932a). (Discarded)

CLUB, cl (tarsi and wings). In July, 1931, a mated wild-type female X-rayed (dosage about 3270 R units) produced among her offspring eight males with club feet. The terminal segments of the tarsi are much malformed, fused, and swollen. The wings show more or less abnormality with a tendency to form extra veins in the radial cell. Club males are about fifty per cent as frequent as their normal sibs. Females fail to oviposit even when caterpillars have been stung by another wasp. A recurrence of club appeared in the offspring of an X-rayed female (dosage about 3500 R units) in the summer of 1934 (P. W. Whiting, 1935b). The hind feet of the club males are flattened and curved down. The antennae droop terminally with deformation of three or four segments. There is a high percentage of pupal inviability, but the males proved fertile. (Discarded)

FOOTLESS, fo (feet). In March, 1933, fifty-two males appeared in the offspring of a heterozygous virgin female which were footless. This mutant type is characterized through a defect

at the end of the fifth tarsal segment involv-
ing lack of claws (Fig. 9). Wings of footless
tend to be more or less wrinkled. Footless
males appear in good numbers from heterozygous
mothers. The females drink honey, but cannot
feed on caterpillars or lay eggs. The males
mate readily but experience much difficulty in
walking and are unable to climb. A recurrence
of this mutant is described by P. W. Whiting
(1935b). This mutation again appeared in the
summer of 1945 in the progeny of an X-rayed
female.

LUMPY, lp (legs). In the summer of 1934 a sin-
gle male, with legs resembling beaded, appeared
in the offspring of a wild-type female that had
been X-rayed (dosage about 4000 R units). The
mutant was discarded soon after its appearance.

WOOZY, wz (legs). A wild-type female X-rayed
(dosage about 4500 R units) in the summer of
1934 produced in her offspring several males
with leg segments abnormally dark. Some of the
male offspring on the other hand were noticed
to have leg segments practically without pig-
ment. The wings in most cases were cupped over
the body. This mutant type was found to be in-
viable at 30° C. and to overlap with normal
wild-type at room temperature. Both sexes were
fertile and of normal viability. (Discarded)
    Many of the foregoing mutations, such as
fused, are semi-lethal and would be lethal ex-
cept for laboratory care in feeding and mating.
However, a number of mutations have occurred
which have their effect at a time or to such a
degree that their possessor cannot eclose or

live as adults. The effects of such factors are visible but completely lethal.

LETHAL NAKED PUPAE, np (pupae). A single female in a pure culture proved heterozygous for this factor. It caused metamorphosis of larvae into undersized naked pupae which attained approximately normal coloration, but died before reaching maturity. This factor (P. W. Whiting, 1921f) proved to be linked with orange (P. W. Whiting, 1932a).

INVIABLE PUPAE, ip (pupae). The following examples will serve to illustrate some of the types of pupae differing in size and bodily proportions and dying on account of lethal or semi-lethal genetic factors (P. W. Whiting, 1934b).

Records of mutant type males segregating from heterozygous mothers not infrequently show more or less numerical deficiency either of wild-type or of the mutant type. When this is statistically significant it is taken to indicate the presence of a linked lethal. Usually no record is made of inviable eggs or larvae, but in some cases dead pupae are recorded. The first case of linkage in Habrobracon was found (P. W. Whiting, 1921f) between orange eyes and a factor, lethal naked pupae, having a lethal effect during the pupal stage. Crossovers were 19.5 per cent and there were 142 pupae to 160 adults indicating that relatively few of the inviables died before pupation. No record was kept of eggs or larvae. The inviable pupae were of approximately normal proportions, perhaps slightly more slender, but they failed to

spin cocoons and ranged in length up to 2.3 millimeters as compared with 2.9 millimeters for the normal wild-type wasp. A recurrence of this mutation occurred in the summer of 1934 (P. W. Whiting, 1935b) in the offspring of a mated wild-type X-rayed female (dosage about 4000 R units).

LETHAL, L (pupae). A locus of three allelic factors for lethal effects, wild-type, La, and Lb has been determined by Schaeffer (1945). The lethal effect is regarded as complementary and probably lies to the right of stubby.

In September, 1943, P. W. Whiting (1943a) described a series of multiple alleles which seem to determine sex in Habrobracon.

SEX GENE OR CHROMOSOME SEGMENT, x (sex). Nine factors are thus far known in the series, and they are designated by the symbols, xa, xb, xc, xd, xe, xf, xg, xh, xi. The tester stocks are designated as xa/xb, xc/xd, xe/xf, xg/xh, and xa/xi. Evidence of allelism of these sex factors is furnished by the fact that they are all closely linked with the gene, fused. The multiple alleles are regarded as differential chromosome segments which have been built up in the early evolution of the Hymenoptera. They may each consist of many genes, which determine the numerous sex differences, structural, functional, and behavioristic, which characterize the Hymenoptera. These genes have the effect that all haploids or homozygous diploids are similar and male, and that heterozygous diploids or combinations of any two different alleles result in females.

Chapter V

RECORDING OF DATA

In recording genetic data in Habrobracon juglandis, P. W. Whiting has simplified the conventional methods. Mutants are symbolized by the first letter or certain letters of the name given the mutant; for example, gl stands for glass, r for reduced, and gz for glaze. If the mutant is recessive to its normal wild-type allele, lower case letters are used; however, in a few cases, the mutant is dominant to its normal allele, and it is then written with the first letter of the symbol capitalized; for example, Y stands for yellow, and Sk for speckled. Normal or the usual wild-type alleles are symbolized by the plus (+) sign. The plus sign is used at all times to indicate the dominant allele of any recessive character, but is omitted from the male and female formulas wherever possible.

The following example will more clearly indicate the method of writing genetic formulas in Habrobracon studies. Let us, for example, cross a homozygous mottled female by a reduced male. The female would be indicated thus, +.mo/+.mo. She is type for reduced and therefore the + sign need not be written in the formula. She is also homozygous for mottled so it would be permissible to merely write mo for her

genetic composition. The male would be indi-
cated thus, r.+. He is type for mottled, there-
fore, the + sign may be omitted from his for-
mula leaving only the r to indicate that he is
both phenotypically and genotypically a mutant
with reduced wings. We may, therefore, indicate
this cross by the formula mo X r. The Fl het-
erozygous females produced from this mating
would be phenotypically type but carry in their
genotype the recessive r and mo. Their formula
would then be +.mo/r.+ which may be written mo/r
indicating that the mo gene was received from
their mother and the r gene from their father.
This again eliminates the + sign and simplifies
the formula. The Fl males produced would, of
course, all be mo. The Fl females, if set as
virgins, will produce four classes of sons in
gametic ratios, +, mo, r, mo.r. For clarity a
period is used to separate the symbols of the
double mutant. Since four classes of sons are
produced by the Fl virgin females we may be
certain that the mutants involved are not al-
lelic. On the other hand if only two classes
appeared as in some eye color crosses it would
indicate that the mutants involved were allelic,
each affecting the same character.

In recording the F2 progeny of the Fl fe-
males, it is advisable to assign each female
involved a number--1, 2, 3, etc., and to letter
each successive vial through which they are
transferred--a, b, c, etc. Thus we have la, lb,
lc, etc., for the first Fl female of the origi-
nal mo.X r cross. The progeny of each female
and for each vial through which she passes may
then be tabulated as in Fig. 10. The entire
progeny from each female in the experiment is

EXPERIMENT 3646

mo X r

No. 1 mo/r F_1 Virgin Set for F_2 Sons Progeny

Vial	+	mo	r	mo.r	Total
1a	3	2	2	0	7
1b	4	3	5	2	14
1c	5	8	6	4	23
1d	8	4	7	5	24
1e	0	3	4	2	9
1f	2	5	0	3	10
1g	5	6	3	1	15
1h	3	4	2	6	15
1i	3	0	2	5	10
Total	33	35	31	28	127

Fig. 10. Individual F_1 female chart showing F_2 male progeny produced per vial and the total F_1 female progeny.

EXPERIMENT 3646

To Test for Linkage of mo and r

mo X r

F_1 mo/r Virgins Set for F_2 Sons

Progeny

Fraternities	+	mo	r	mo.r	Total
3646.1	33	35	31	28	127
3646.2	39	26	32	28	125
3646.3	29	26	20	32	107
3646.4	26	29	27	33	115
3646.5	35	26	37	37	135
3646.6	42	37	47	27	153
3646.7	29	28	35	26	118
3646.8	34	24	41	31	130
	267	231	270	242	1010

Conclusion: mo and r segregate independently.

Fig. 11. Master sheet of F_1 females showing the total progeny in the experiment and conclusions.

then tabulated on a master sheet (Fig. 11). Each female carries her own number and to it is added the number of the experiment and the year in which it was performed. Thus in the number 3646.8 the 36 represents the experiment, the 46 the year in which the experiment was performed, and the .8 the eighth Fl female set in the experiment.

This method of recording data is suggested by the writer as it offers the most convenient and accurate way of keeping track at all times of each Fl female and her progeny involved in any experiment.

Chapter VI

SEX CONDITIONS

Like other hymenopterans, Habrobracon juglandis is parthenogenetic in that males are produced from unfertilized eggs, so that the males possess only a single set of chromosomes. Females which normally develop only from fertilized eggs have a double set of chromosomes and are diploid. The haploid males are extremely useful in genetic studies, since their appearance indicates their exact genetic composition. The females, being diploid, may bear more factors than they show, since the effects of certain genes may mask those of others, which are recessive. In order to bring recessive alleles to light, females are set unmated on Ephestia caterpillars and allowed to lay eggs. The resulting sons exhibit the effects of all the genes carried by their mothers, since during egg maturation the paired chromosomes of the females separate giving dominant genes to some eggs and their recessive alleles to others. For this reason, the wasp is an especially advantageous animal for genetic studies, since in one generation only, all of the genic characters possessed by the stock are brought to light.

Occasionally females from unfertilized eggs (thelytoky) are found in fraternities which normally produce males from unfertilized eggs

(arrhenotoky). These males and females from un-
fertilized eggs have been termed "impaternate"
by Ray Lankaster (1919) to differentiate them
from the parthenogenetic virgin mother. Breed-
ing tests show that impaternate females are nor-
mal diploids. P. W. Whiting (1924a) has ex-
plained their production from unfertilized eggs
by the assumption that the second maturation
division of the oöcyte is suppressed. If this
assumption is true and the impaternate females
occur among the F2 from a cross involving mutant
characters, their genotypes, as indicated by
their appearance and that of their offspring,
are of interest in ascertaining whether the
first division of the oöcyte from which they
were formed was equational or reductional for
the locus or loci involved (K. G. Speicher,
1934). If the Fl female producing an impater-
nate daughter is heterozygous for a recessive
factor and the first oöcyte division is reduc-
tional for the locus of that factor, the impa-
ternate daughter will be homozygous for either
the recessive or its type allele. If the first
oöcyte division is equational, the impaternate
daughter will be phenotypically wild-type.
Breeding tests are necessary to distinguish im-
paternate females resulting from an equational
division from those receiving the type allele
from a reductional division.

Diploid males of biparental inheritance reg-
ularly occur in related stocks. These sterile
(or near-sterile) males are diploid, developing
like females from fertilized eggs. The haploid
males have been called uniparental and azygous
in contrast to the biparental zygous males and
females. The offspring of these diploid males

crossed with recessive females are triploid fe-
males showing the dominant traits of their dip-
loid fathers. There is no evidence of inter-
sexuality in diploid males or in triploid fe-
males unless the reduced size of ovaries and
near sterility of the latter indicate this.
Moreover their reproductive reactions are en-
tirely normal, the diploid males mating readily
and the triploid females stinging caterpillars
and feeding and ovipositing upon them.

Unmated females produce azygous sons only.
Mated females produce azygous sons from unfer-
tilized eggs but in smaller numbers than do un-
mated females. They also produce zygous bipa-
rental offspring from fertilized eggs. Whether
the biparental offspring shall be daughters on-
ly or both sons and daughters depends upon the
relationship of the male and female used in the
mating. If the male is from a stock unrelated
to the female all the biparental offspring are
daughters, but if the male comes from a related
stock, biparental sons as well as daughters are
produced.

In general the azygous and biparental off-
spring from a mated female occur in the same
ratio from the different vials through which
the female is transferred (a, b, c, d, etc.)
until her supply of sperm is exhausted. In sub-
sequent vials (e, f, g, etc.), azygous sons only
appear.

Biparental males cannot conveniently be sep-
arated from their azygous brothers unless the
mother has a recessive trait and the father has
the allelic dominant. Orange-eyed females
crossed with wild-type (black-eyed) males pro-
duce black-eyed daughters and orange-eyed azy-

gous sons. If biparental sons are produced
they may be readily separated from their azygous
brothers by their black eyes.

Fertilized eggs may be "female-producing" or
"male-producing," the latter occurring only if
parents are related. "Male-producing" ferti-
lized eggs are less likely to hatch than "fe-
male-producing." Consequently there are more
"bad eggs" and fewer biparental offspring if the
mating has been with a related male, since the
percentage of eggs fertilized is the same wheth-
er the male is related or unrelated. Biparen-
tal male larvae are also less likely to mature
than female larvae. This further reduces off-
spring from related parents.

Two types of male sterility may be distin-
guished in Habrobracon. If the eggs are not
fertilized, the mated female breeds like an un-
mated female, producing a large number of azy-
gous sons. This occurs in the case of matings
with biparental males which produce diploid
sperm rarely capable of fertilizing eggs. There
are also males with abortive sperm ducts or
testes which may readily be mated but transmit
no sperm. Recent evidence indicates that sperm
may to some extent be inactivated by high dos-
ages of X-rays, so that they are unable to pen-
etrate the eggs.

Cytological studies indicate that there are
ten chromosomes in the normal haploid male (Fig.
12) and twenty in the biparental diploid male
(Fig. 12). The normal female has twenty chro-
mosomes (Fig. 12), while the daughters of normal
mothers and biparental fathers have an as yet
undetermined but considerably larger number, in
all probability thirty. A spermatogonial study
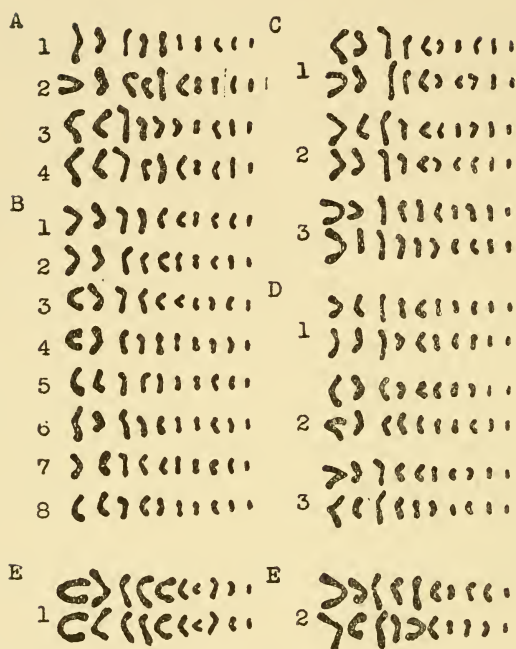
Fig. 12. Metaphase chromosome complexes. From left to right there are shown in decreasing order of magnitude: one V, one L, one J, one L, three V's, one J, one which is often rod-like but may be a V, and one rod. M. Torvik-Greb, 1935.

A, 1-4. Spermatogonial complexes of haploid males.
B, 1-8. Second spermatocyte complexes of haploid males.
C, 1-3. Spermatogonial complexes of diploid males.
D, 1-3. Second spermatocyte complexes of diploid males.
E, 1-2. Oögonial complexes of diploid females.

X 3,280

has been made in both the normal and biparental
males. Following the spermatogonial divisions,
both kinds of males show an abortive first mat-
uration division--a small bit of the cytoplasm
being pinched off at the narrow end of a pear-
shaped cell. This division of the sperm cell in
the male is comparable to the reduction or mei-
otic division of the egg, at which time the
paired chromosomes separate, forming abortive
polar bodies and one haploid egg nucleus. Eggs
if unfertilized by sperm will hatch into normal
haploid males. If fertilized, they will pro-
duce normal diploid females; and in abnormal
cases, diploid biparental males.

It has been shown (Speicher, 1935; Risman,
1941) that diploid males have much larger cells
than diploid females, while haploid males have
cells approaching the diploid female size. It
seems possible that large cell size might be
responsible for the high diploid male mortality
and that a demonstrable difference in cell size
might appear between diploid males differing in
mortality.

In developing Habrobracon it is observed that
each bristle on a wing surface corresponds to
and gives indication of the presence of a wing
surface cell (Speicher, 1935). Since each cell
of the single layer forming the upper surface of
the wing bears a single bristle (microchaeta),
variations in cell size produce proportional
variation in dispersal of bristles. Thus, if
fewer michochaetae are noted per unit area
larger cells are present in the wing surface.
A tendency toward larger cell size in diploid
male material with higher mortality is indi-
cated in microchaetal evidence. The tendency is

not extreme in the adult animals studied presumably because extreme types did not survive to the adult stage. Evidence of selective action of mortality is shown by differences between frequency distribution curves of diploid males and the curves of more viable types.

In all material investigated (Grosch, 1945) diploid male cell size was significantly larger than female cell size. This is shown by the number of microchaetae per unit area of wing surface and by measurements of eye facets. To explain diploid male mortality it is suggested that doubled gene situations in the diploid male, homozygous for a sex allele, might function poorly under the surface-volume relationship of the large diploid male cell. The large size of diploid male cells may itself be the result of gene duplication. The system which raises haploid male cells to a size comparable with diploid female cells may be increased in activity when its determiners are doubled in the homozygous sex allele condition of the diploid male.

No statistically significant differences are shown in body length between diploid males and females, and observations indicate that diploid males do not exhibit gigantism. Haploid male mean body length is shown to be consistently less than that of diploid wasps, and this is taken as indication of the tendency toward dwarfism of the haploid male. Wing length corresponds to body length in all classes.

Larger eyes of the male are a secondary sex character not affected by cell size differences. This sex character is not as clear cut as antennal length. Long antennae of the male are a

secondary sex character. In no diploid males
has there been a significant shortening of an-
tennae which would be considered a tendency to-
ward intersexuality. Such stability of second-
ary sex characters is discussed on the basis of
the sex allele being a differential chromosome
segment. Female antennae are shorter chiefly
because of fewer segments. Diploid males have
a tendency toward fewer and longer antennal seg-
ments than haploid males. Fewer antennal seg-
ments in the diploid male are not regarded as
the result of intersexuality but as an indirect
effect of chromosome number.

Definite types of reactions characteristic
of sex are found in Habrobracon. The females
sting caterpillars on which they subsequently
feed and lay their eggs. The males are entire-
ly indifferent to caterpillars, but they show
characteristic reactions towards females, such
as flipping wings, mounting, and beating with
wings and antennae in the process of mating.

Gynanders (sex-mosaic individuals) occasion-
ally appear in bisexual fraternities. Gynandro-
morphic offspring from a recessive female by a
dominant male show the maternal trait in the
male (haploid) parts, the paternal trait in the
female (diploid) parts. This evidence is con-
sistent with the theory of egg binuclearity.
Fertilization of one nucleus results in the fe-
male parts; development of the other without
fertilization results in the male parts. Gynan-
ders may have male heads, female abdomens, or
the reverse; one side may be male, the other fe-
male; anterior left and posterior right may be
of one sex, the remainder of the other sex; male
islands may occur in female regions or female

islands in male regions. When genitalia are
mixed in sex, there may be a full set of male
structures and a half set of female structures.
Two of these cases have been published (P. W.
Whiting and A. R. Whiting, 1927). Gynanders in-
dicate that the various sexual reactions are
determined by the head rather than by the repro-
ductive organs of the animal. Those with male
heads and female abdomens react towards females
but are indifferent to caterpillars; while those
with female heads and male abdomens pay no at-
tention to females but respond to caterpillars.
Gynanders with mixed heads act in general either
like males or like females. Gynandromorphic be-
havior is not all as clear-cut as the head and
abdomen variations described above. Some show
momentary sex-reversal for one or more brief
periods of time, and therefore, behave sometimes
like females and sometimes like males. There
is also a bisexual type of individual which at-
tempts to sting caterpillars as well as to mate
with females; and there is also a type which has
been termed "wires crossed." These individuals
attempt to mate with caterpillars and to sting
females. All these various irregularities of
behavior are thought to be caused by the mosaic
character of the sensory and nervous systems
rather than to any hormonal action.

Very little evidence of intersexuality has
been found in Habrobracon so far. One mutant
type, gynoid, has been found, the gene for which
causes haploid males to be weakly intersexual.
Gynoid females are indistinguishable from wild-
type. The trait acts as a recessive in hetero-
zygous diploid males. Gynoid males are similar
to normal males in internal structure and in

external genitalia. Their ocelli are large re-
sembling those of normal males. Their normal
male instincts indicate that the brain is struc-
turally as in the male, since mating reactions
in Habrobracon are determined by the brain.
Sclerotization of the abdomen is progressively
heavier anteriorly, approximating the condition
found in the female. Antennae of normal males
have about twenty-one segments in the flagellum,
those of females usually not more than fourteen.
In gynoid males the segments are reduced in num-
ber to that of the female, although they are not
quite as short and thick. Superficially a gyn-
oid male suggests a sex-mosaic or gynander with
female head and male abdomen. Certain struc-
tures intergrade, the body is approximately sym-
metrical with all parts presumably of the same
genetic constitution, and the type is perpetu-
ated as a pure-breeding form.

Nine intersexual females have recently oc-
curred among the offspring of a single female.
Superficially these appear to be the reverse of
the gynoid males, being more masculine anterior-
ly and more feminine posteriorly. The heads are
characteristically male having large ocelli and
long antennae, the segments ranging from eight-
een to twenty-one with twenty as the mode.
Tests made on five of the nine showed indiffer-
ence to caterpillars and vigorous attempts to
mate with females, indicating the brain to be
structurally male. Abdominal sclerotization is
male-like anteriorly. The first and second ter-
gites are thin and the anterior sternal thick-
enings small. Sclerotization is progressively
heavier posteriorly and sternal thickenings be-
come elongate, approximating the condition of

the female. Like gynoid, these intersexes dif-
fer from sex mosaics in being approximately sym-
metrical and similar to each other. They pos-
sess intermediate sex characters and occur in a
group in one fraternity as if caused by a sin-
gle hereditary factor.

The existing data must be regarded as inade-
quate to prove whether these intersexes are the
result of a modification of the normal sex-dif-
ferentiating factor or whether, like gynoid,
they are the result of an independent change.
It is questionable whether the diverse effects
of gynoid antennae and abdominal sclerotization
should be regarded as multiple effects of a sin-
gle gene. Gynoid may possibly be a transloca-
tion from the differential segment determining
sex. In a male with the sex allele in the nor-
mal position this might give a complementary
feminizing effect causing intersexuality.

Mosaics also occur which apparently possess
either one sex or the other; however, these too
exhibit interesting peculiarities. Genetic ev-
idence indicates that mosaics, with but few ex-
ceptions, arise from binucleate eggs. The two
nuclei are assumed to be the products of the
second oöcyte division. In the case of gynan-
ders one of the nuclei is fertilized and gives
rise to the female parts while the unfertilized
nucleus produces the male parts. Cell descend-
ants of each of the two nuclei tend to be more
or less segregated in different regions of the
embryonic syncytium and consequently the genet-
ically diverse regions may be roughly separated
by a plane. This plane of division may appar-
ently lie at any angle to the axis of the body
and may separate proportions varying from ap-

proximate equality to such decided inequality that tissues of either type may represent but a minute portion of the specimen. Furthermore, the region on either side of this plane may contain tissues of the opposite genetic constitution indicating more or less wandering of nuclei in the embryonic syncytium. Occasionally lack of segregation may be so extreme that the resulting mosaic is an irregular patchwork. Readjustments during later embryonic development may, moreover, cause intermingling of adjacent tissues differing genetically.

In certain normal wasps, there occur two non-allelic, recessive genes both of which cause the eyes to be whitened. For convenience, these genes are called white and ivory. One interesting combination of these colors occurs in the mosaic compound eye, one section of the eye being genetically white, the other genetically ivory. Such an eye might be expected to look uniformly white; however, such is not the case. The white, non-ivory region remains white and is sharply marked off from the ivory, non-white region by a black border which grades imperceptibly into the ivory (Fig. 13) (A. R. Whiting, 1933b). The double dominant character is reconstituted in the region where the two recessives are in contact even though there is no diploid tissue present there. This phenomenon is thought to be the result of the diffusion of some substance from the white region into the ivory. Another instance of the effect of one gene upon another is exhibited in the progeny of a female heterozygous for ivory and cantaloup eye colors. Such a female set as a virgin may produce, in addition to the four genotypes of sons regular-
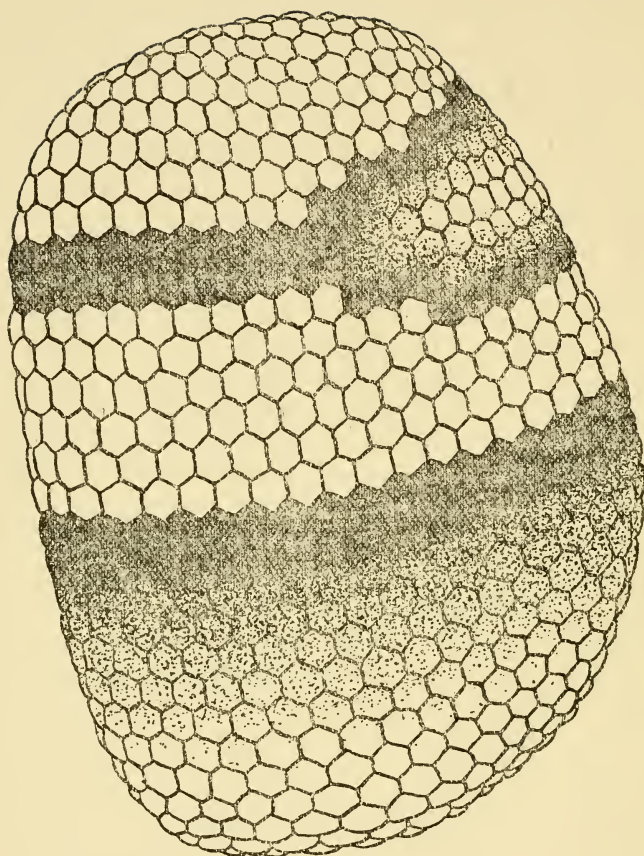
Fig. 13 . Right compound eye of male mosaic for
white and ivory. The double dominant character
is reconstituted in the region where the two
recessives are in contact.

X 208.

ly expected, a male with ivory, non-cantaloup and non-ivory, cantaloup regions in the same eye. In this case the genetically ivory region bordering the cantaloup changes to wild-type black, a phenotypic complementary effect the result of soaking through into the ivory region of some product dependent upon the dominant allele to ivory in the cantaloup region. Similarly, feminization occurs in the genitalia of a high proportion of haploid mosaic males, the result of a complementary effect, an interaction between sex factors, differing in the two regions, X and Y. These "gynandroid" males (P. W. Whiting, Greb, and Speicher, 1934) develop from unfertilized binucleate eggs in which the sex alleles have been segregated at maturation into the different nuclei. They are, therefore, haploid throughout. They suggest gynanders (haplo-diploid male-female mosaics) which also arise from binucleate eggs, but in the formation of a gynander one of the nuclei must be fertilized to originate the female regions. Gynandroids are entirely male in appearance except for the relatively small feminized structures added to the male genitalia, usually on one side only (Fig. 14). The male genitalia may show reduplication of parts. Gynanders, on the other hand, have extensive female regions of the body, while the genitalia may be either male, female, or mixed. In the latter case there is usually a complete set of male parts but no reduplication. The female structures tend to be lateral on one side only and anterior to the male organs, with appendages of full length. Interpretation of gynandroidism as a complementary effect led to the conclusion that females are heterozygous and

Fig. 14. Ventral view of the genitalia of a
gynander, a male-female mosaic. A complete
set of male genitalia is present. The left
sensory gonapophysis of normal length, and
two elements of the sting, are the female
structures. X 120. P. W. Whiting, 1940a.

Fig. 15. Dorsal view of male, mosaic for long
(antennae and wings), for narrow (wings), and for
cantaloup (eyes).   P. W. Whiting,   1934c.

X 20.

that normal males are X and Y with equal fre-
quency.

The feminized structures just mentioned do
not appear on all mosaics, for in many the line
of mosaicism does not pass through the genital-
ia. It has also been found, however, that these
structures do not always occur in mosaics even
when the line does bisect the body (Fig. 15).
These facts have led to the supposition that in
Habrobracon there are several kinds of males,
genetically distinct for sex-determining fac-
tors but phenotypically similar. When tissues
differing in sex-determining factors adjoin in
a haploid mosaic male, one influences the other,
and traits characteristic of diploid tissue are
the result.

CHAPTER VII

SEX DETERMINATION

Genetic research with the wasp Habrobracon juglandis was begun at the University of Pennsylvania in 1916 by P. W. Whiting. Many phases of this work have been developed since that time but the central problem has always been that of sex determination.

In 1845 Dzierzon put forth the theory that in the honey bee, drones (males) develop from unfertilized eggs while workers and queens (females) come from fertilized eggs. This theory was based on the fact that unmated and old queens produce drone broods and that race-crossing results in drones like the maternal race while the daughters are hybrid. Dzierzon (1854) stated that the drones of the second generation from a cross resemble either the paternal or the maternal race and that these two types occur in equal numbers. He, therefore, glimpsed the fundamental gametic ratio twelve years before Mendel published his paper on peas. Dzierzon's Law applies to other insects of the order Hymenoptera, including wasps, ants, ichneumon-flies, chalcis-flies, and saw-flies, but many exceptions occur. P. W. Whiting (1918) working with the ichneumonoid wasp, Habrobracon, found that in this form also haploid males are pro-

duced from unfertilized eggs, and females from fertilized eggs.

Nachtsheim in 1913 had shown that somatic cells of the honey bee possess the haploid number of chromosomes in the case of the male, and the diploid number in the case of the female. Sex determination in the Hymenoptera was then assumed to rest upon the possession of one sex chromosome in the haploid male or two in the diploid female.

Bridges (1925), discussing sex determination in the bees and wasps stated that it was the outstanding unsolved puzzle, although before the genic balance theory it seemed one of the clearest and simplest of cases.

The explanation of sex determination in Habrobracon was further complicated when diploid males were found to occur occasionally. Tests made with the first mutant type, the recessive orange eye-color, demonstrated that three types of individuals, haploid males from unfertilized eggs and diploid males and females from fertilized eggs, occur regularly in the species when parents are related. When orange females were crossed with the wild-type black-eyed males, there appeared not only the expected black-eyed heterozygous females from fertilized eggs and orange haploid males from unfertilized eggs, but also a smaller group of "anomalous" sterile or almost sterile males which were black-eyed. Since males were then regarded as necessarily haploid, these "patroclinous" sons were thought to be either androgenetic or mosaic in origin, having arisen through failure of syngamy (P. W. Whiting, 1921a).

This view persisted until 1925 when it was

shown (P. W. Whiting and A. R. Whiting, 1925;
A. R. Whiting, 1926, 1927, 1928a) that "patroc-
linous" males were really of biparental inheri-
tance, receiving dominant traits of both par-
ents. Genetic search was then made for a gene
that they might possess in the simplex condi-
tion, occupying an odd X chromosome or a dif-
ferential X region in one of the pairs. No such
gene was found. Later cytological work (Torvik-
Greb, 1935) indicated no visible difference be-
tween the ten pairs of chromosomes of these bi-
parental males and the ten pairs characteristic
of females. According to the principle of gen-
ic balance, if the genetic complex of the fe-
male were merely that of the male doubled, the
ratio of male-producing to female-producing
genes should remain the same. There should then
be but one sex, the male, because any multiple
of the haploid complex would make but a slight
change in size or proportion of parts, not af-
fecting such a radical transformation as is in-
volved in sex difference.

In 1933 (P. W. Whiting, 1933e,f) the hypoth-
esis of complementary factors was suggested and
shortly thereafter proved true by sex-linkage.
According to this hypothesis the female is het-
erozygous for a pair of sex factors, called X/Y
at the time, and she produces two kinds of hap-
loid males from unfertilized eggs, X and Y.
Mating with a closely related X male gives dip-
loid zygotes, male-producing X/X, female-produc-
ing X/Y, and male-producing Y/Y. The male-pro-
ducing homozygotes are much less viable than
the female-producing heterozygotes, accounting
for the low frequency of diploid males.

A supplementary hypothesis of differential

maturation was proposed by P. W. Whiting (1933e)
to explain the absence of diploid males in out-
crosses. In these crosses, the egg, being in
an indecisive stage of reduction division at
the time of fertilization, would eliminate into
the polar body the same sex factor that was be-
ing carried in by the sperm, and thus the fer-
tilized egg would always be heterozygous for
the sex factor, that is, female-producing. In
close-crosses, however, some influence seemed
to prevent this mechanism of differential matu-
ration from affecting the disposal of the like
sex factor; and so there were some diploids
which, being homozygous for the sex factor,
were males.

It had been noted previously (A. R. Whiting,
1925) that females mated to related males were
less fecund than those mated to unrelated males.
This appeared to be the result of excess bad
eggs in close-cross fraternities. On the basis
of the theory of complementary factors, these
eggs are considered to be male-producing zy-
gotes, and increased fecundity in out-crosses
the result of a replacement of these by female-
producing zygotes.

This hypothesis of complementary factors was
suggested after study of complementary effects
in eye-color and in genitalia of haploid mosaic
males, which occur occasionally among the prog-
eny of unmated females heterozygous for mutant
traits (P. W. Whiting, Greb, and Speicher, 1934).
Interpretation of gynandroidism as a complemen-
tary effect led to the conclusion that females
are heterozygous and that normal males are X
and Y with equal frequency. This hypothesis of
complementary factors was proved true by sex-

linkage of the recessive gene, fused (P. W. Whiting, 1935a,c).

Snell, in 1935, presented evidence based on Bostian's (1934) published data that would support a theory of independently segregating multiple sex factors. He suggested that heterozygosity of one or more of these factors results in a female, but homozygosity of all produces a diploid male (Snell, 1935).

In 1939 P. W. Whiting proposed a theory of sex determination in Habrobracon based on multiple alleles (P. W. Whiting, 1939). In this theory, the explanation of sex inheritance in close-crosses is essentially the same as that proposed by P. W. Whiting in 1933. The females are heterozygous for the sex factor, the haploid males are of different types as regards the sex factor, and the diploid males are homozygous for the two sex alleles involved. The importance of the multiple allele theory is the fact that it gives an explanation of sex determination in outcrosses, where no diploid males are produced. The upper case letters X and Y were then abandoned as sex symbols, and lower case x was taken to indicate the sex factor exclusively. The x accompanied by certain letters of the alphabet now designates the various alleles in the series--xa, xb, xc, etc. According to the multiple allele theory any heterozygote for two members of the series, xa, xb, xc, etc., is female, any homozygote or azygote (haploid) is male. Given n alleles in the series, there should be possible n different haploid males, n corresponding diploid males and $(n^2-n)/2$ females.

With respect to the three classes of offspring--females, diploid males, and haploid

males, different ratios have been considered in the publications. At first, ratio of females among total progeny was used, but this was soon given up in favor of ratio of total diploids. Ratio of males among diploids was also calculated. It was noted that these two ratios were negatively correlated and that outcrossed females had higher fecundity than close-crossed. The latter fact, checked later by egg counts, showed that low viability of diploid males, together with presence or absence of male-producing zygotes rather than difference in ratios of eggs fertilized, lies at the basis of the negative correlation. Since, according to the multiple allele theory, male-producing zygotes are formed in close-crosses with frequency equal to female-producing, the ratio of diploid males to females may be used to express the relative viability of the diploid males.

Bostian (1939) gave the first evidence supporting the multiple sex allele theory. He selected for independent segregation of fused and sex for twenty generations, while constantly inbreeding. He was unable to establish a line breeding true for independent segregation of sex and fused, although on the basis of Snell's hypothesis, the establishment of homozygous sex factors on the chromosome bearing fused would allow for such a condition. The results of this work indicate that there were triple sex alleles present. A review by P. W. Whiting (1940c) of the available data further supports and confirms the multiple allele theory of sex determination.

The multiple allele theory of sex determination in Habrobracon has been exhaustively tested

(P. W. Whiting, 1940c, 1943a). Laboratory stocks
have been analyzed for sex factors. Technique
consisted in selecting one stock, designating
its sex alleles as xa/xb, and introducing into
it a recessive gene. If all significantly large
fraternities from crosses of recessive females
of this stock to dominant males of an unknown
stock contained dominant males (diploid), as
well as the recessive males (haploid) and domi-
nant females (diploid), the Pl male stock was
considered to have the same sex alleles, xa/xb.
If no dominant males (diploid) appeared in any
of the fraternities, the Pl male stock was re-
garded as having different alleles--for example,
xc/xd. If only one-half the fraternities in-
cluded dominant males, the Pl male stock was
considered to have one allele in common with
xa/xb--for example, xa/xi. Recessive genes were
introduced into each new stock as it was ana-
lyzed for sex factors, and "tester" stocks were
made up for future use.

Nine factors are thus far known in the series
(xa through xi), and the tester stocks are des-
ignated xa/xb, xc/xd, xe/xf, xg/xh, and xa/xi.
Evidence of allelism of these sex factors is
furnished by the fact that they are all closely
linked with the gene, fused. Lack of diploid
sons and equality of fused and non-fused daugh-
ters from crosses of stocks tentatively desig-
nated as having different sex alleles in the x
series proves the sex factors to be different,
but their linkage with fused indicates their
allelism.

The multiple alleles are regarded as differ-
ential chromosome segments which have been built
up in the early evolution of the Hymenoptera.

They are necessarily associated with haploid parthenogenesis, and consist of many genes determining the numerous sex differences, structural, functional, and behavioristic, characterizing Hymenoptera. These genes have, in the aggregate, duplicate effects such that all haploids or homozygous diploids are similar and male, but combinations of any two different alleles result in females (heterozygous dominants), likewise all similar.

This principle of sex determination may be illustrated by the following example. An xa/xb female homozygous for the autosomal recessive gene, veinless, but heterozygous for fused and having fused associated with xb may be crossed with a non-veinless xb fused male (Fig. 16A). The recessive veinless serves to mark the haploid sons which are fused and non-fused in equal numbers. The diploid offspring, whether males or females, will be non-veinless. Among the daughters, xa/xb, the non-crossovers will be wild-type, the crossovers fused, but among the diploid sons, xb/xb, the reverse condition exists. Since crossing over between x and fused is about ten per cent, fused will show great deficiency among the daughters, great excess among the diploid sons. If both parents have fused associated with xa, the offspring occur in the same ratio (Fig. 16B), but if fused is associated with xa in one parent and with xb in the other, the ratios of fused among the two types of diploid offspring are reversed (Fig. 16C and D) giving an excess of fused among the daughters, deficiency among the sons. Thus there are four different arrangements possible

CROSSES INVOLVING SEX DETERMINATION

MOTHER	FATHER	HAPLOID SONS		DAUGHTERS xa/xb or xa/xc and xb/xc-		DIPLOID SONS AND EXCESS BAD EGGS xa/xa or xb/xb	
		vl	vl.fu	+/fu	fu/fu	+/fu	fu/fu
A $\dfrac{vl}{vl}\dfrac{xbfu}{xa+}$	xbfu	5	5	9	1	1	9
B $\dfrac{vl}{vl}\dfrac{xafu}{xc+}$	xafu	5	5	9	1	1	9
C $\dfrac{vl}{vl}\dfrac{xa+}{xbfu}$	xafu	5	5	1	9	9	1
D $\dfrac{vl}{vl}\dfrac{xb+}{xafu}$	xbfu	5	5	1	9	9	1
E $\dfrac{vl}{vl}\dfrac{xbfu}{xa+}$	xcfu	5	5	10	10	0	0

Fig. 16. Ratios of offspring expected according to various arrangements of sex alleles in crosses of veinless females heterozygous for fused by fused males. P.W.Whiting, 1943a.

for x and fused but only two phenotypically separable ratios.

Fraternities of the close-cross type may now be called two-allele fraternities, those of the outcross type three or four-allele fraternities. A third allele brought into the cross by a fused male, xc.fu for example, always masks sex-linkage, since all diploid offspring are heterozygous for x and hence female, fused and nonfused in approximately equal numbers (Fig. 16E). Diploid males reappear with inbreeding, and their presence is always associated with obvious sex-linkage of fused as shown by Bostian (1939).

Sex determination, is in a sense, polygenic, but because of no crossing-over within the segment, the various groups of genes act as a single series of allelic factors. Just as the many sex-producing genes distributed among the X-chromosome of Drosophila segregate as a unit from the Y without crossing-over, so the dominant female-producing genes and the recessive male-producing genes of the x factor in Habrobracon segregate without crossing-over from their homologues. Males, as determined by the various alleles (whether azygous or homozygous), or females as determined by any of the heterozygous combinations, are always phenotypically similar (P. W. Whiting, 1945b).

Whether the sex alleles ever mutate has not been established with certainty. They appear to be very stable. Extensive breeding within a two-allele stock has resulted in two-allele fraternities almost exclusively, as evidenced by the presence of diploid males. With certain very rare exceptions, the fraternities lacking diploid males are small, so that the lack is

evidently the result of error in sampling. The rare exceptions, which were not adequately tested, may have been the result of contamination, though this is unlikely, or to some combination of factors reducing diploid male viability, or to mutation in a sex allele itself.

The nature and evolution of the sex factor, x, the differential segment, may now be considered. Mutant genes are known to cross over both to the left and to the right of x, hence x is interstitial, but so far no crossing over within x has been noted. If, however, crossing over within x did occur, x would be inconstant, xa would not remain distinct from xb, or xb from xc, etc. The work of Horn (1943a,b) demonstrates that F2 males segregating from crosses of xa/xb with xe/xf stocks are still xa, xb, xe, or xf, that they all sire diploid sons, and that those that were xa or xb sire diploid sons by xa/xb females and not by xe/xf females and the reverse (as shown by linkage with fused). It may be concluded, therefore, that there is no crossing over within x; or perhaps the rare "mutations" of x, if such actually occur, may be crossovers.

Whether or not Whiting's multiple allele theory of sex determination is applicable to the Hymenoptera in general is as yet a question. Were it not for parthenogenesis, this complementary scheme might never have been proposed. Diploid males have been shown in two other species of Habrobracon (Speicher and Speicher, 1940; Inaba, 1939), but so far no one has applied breeding and observational tests that

might reveal them elsewhere; and no evidence has yet appeared that prevents the extension of the multiple allele theory to the Hymenoptera in general.

Chapter VIII

LINKAGE

So far in Habrobracon juglandis there have occurred about one hundred known mutations each involving a different gene. Since the wasp has only ten pairs of chromosomes, it is apparent that each chromosome must bear a number of different genes. The position of each gene and its allele or alleles is definite; that is, each pair of alleles always occupies the same locus on the same pair of chromosomes in diploid wasps. Of course, in haploid males, only a single set of chromosomes is present. Crosses have been made involving these mutant types in various ways to test the principles of heredity. Linkage tests are made by crossing various mutant types and counting the F2 haploid sons of the unmated Fl heterozygous females. The azygotic ratios thus obtained approximate gametic ratios except as they may be affected by differential viability of the various haploid genotypes. Linkage tests thus made show that maps are very long in crossover units. On this account, despite much work extending over several years, there is as yet no approximation of linkage groups to the number ten, corresponding to the haploid set of chromosomes.

If certain gene mutations, such as speckled, reduced, and glass, occur more frequently in

combination than they do separately, the genes
are said to be linked; and therefore, borne on
the same chromosome. At the present time four
linkage groups (Fig. 17) are recognizable.
These groups may occupy four different chromo-
somes or they may be found to be linked and
thus occupy fewer than four chromosomes. In
1933 fifty genes were known, and they comprised
eight linkage groups. It was thought then that
each group represented a different chromosome.
However, since that time, new genes have come
to light that have linked the second and fourth
groups, others have linked the fourth and fifth,
others have linked the fifth and eighth, and
still others have linked the first and third.
It is apparent, therefore, that while the num-
ber of known genes has increased, the number of
linkage groups has decreased.

There is one unusually long sex chromosome
known to be at least five hundred units in
length. Starting at the left end of this sex
chromosome, designated linkage group one (I),
the genes are arranged in the order: speckled,
reduced, glass, etc. Helsel (1943, 1944) con-
ducted experiments in order to check recombina-
tion and interference in this region, and to
compensate for any viability disturbance or po-
sition effects introduced the genes in all pos-
sible combinations. She reported 12.07 per
cent crossing over between speckled and re-
duced, and 12.69 per cent crossing over between
reduced and glass. Coincidence is 0.264, but
varies markedly as the genes are introduced in
different combinations. Linkage of these genes
had been shown (P. W. Whiting, and Benkert,
1934) with about 13 per cent crossing over be-

HABROBRACON LINKAGE GROUPS

Group I

```
Sk -- 13 --  r
r  -- 15 -- gl
gl -- 37 -- fu
x  -- 10 -- fu
fu -- 24 -- sb
sb -- 30 -- bl
bl -- 14 -- le
le --  6 --  c
c  -- 15 --  l
l  --  3 --  n
n  --  9 -- ho
ho --  8 -- vl
vl -- 12 -- cw
cw --  5 -- ro
ro -- 12 -- bu
bu -- 37 -- dr
dr -- 17 -- cr
cr -- 41 -- sl
sl --  0 -- co
co -- 33 -- ct
ct -- 22 -- rd
rd -- 40 -- gy
gy --  4 -- ac
ac --  4 -- el
el
```

Group II

```
k -- 28 --  m
m --  8 --  o
o
```

Group III

```
bk -- 25 -- st
st --  9 -- wh
wh -- 10 -- at
pl -- .3 -- wh
at -- 22 -- st
```

Group IV

```
sv -- 12 -- td
td -- 27 -- ma
sw -- 24 -- sv
ma
```

Fig. 17. Linear arrangement of genes with crossover percentages. For additional data see Table II.

tween speckled and reduced, and about 15 per
cent crossing over between reduced and glass.
The sex gene lies to the right of glass and is
followed by fused and stubby, which have been
shown to be sex-linked. The strength of the
sex linkage of fused has been shown to vary
from 8.6 per cent to 17.6 per cent crossing
over (P. W. Whiting, 1940e). Hager (1941) work-
ing with orange-eyed females heterozygous for
stubby, showed crossing over to be 37.5 per
cent between stubby and the sex gene, and 24.2
per cent between stubby and fused. Linkage
across the sex gene indicates that speckled
and stubby appear to segregate independently,
and no linkage between speckled and fused is
noted. Stubby shows very slight, if any, link-
age with reduced or with glass. A study by
P. W. Whiting and Benkert (1934) indicates link-
age between reduced and fused with 45.5 per
cent crossovers. Linkage between fused and
glass, with 41.7 per cent recombinations, sug-
gests that glass is nearer fused than is re-
duced. Recent experiments bear out this con-
clusion. No conclusive evidence is as yet
available for the sex linkage of glass, which
may be very loose or may be masked by a third
allele and by viability differences. A linkage
map of regions near the sex gene with approxi-
mate intervals may be constructed as follows:

Sk --13-- r --15-- gl x --10-- fu --24-- sb
               ------37-----
               ---------35---------

Anderson and P. W. Whiting (1939) reported a
"cantaloup" group of 14 loci with a map dis-

tance of 187 units lying to the right of stubby.
Klotz (1940) reported on linkage tests made
with veinless, lying approximately in the cen-
ter of this group. Veinless and honey are
linked with a crossover value of approximately
7.5 per cent (Clark, 1942). Veinless and stub-
by show no crossing over and are, therefore,
thought to be not linked. Veinless and lemon
show a linkage value of approximately 32.3 per
cent. Veinless and black show a linkage value
of approximately 34.6 per cent. These data in-
dicate that the factors, veinless, honey, lemon,
and black, are located on the same chromosome.
Crossover percentages are 14 between black and
lemon, six between lemon and cantaloup, and 19
between cantaloup and honey (A. R. Whiting,
1939b). Black is linked to stubby with a cross-
over value of approximately 30 per cent. Vein-
less and cantaloup are linked with approximate-
ly 30.6 per cent crossing over. Long and vein-
less show a linkage value of approximately 17.0
per cent. Long and cantaloup show a linkage
value of approximately 14.5 per cent. Inter-
ference is evident in the three point cross be-
tween cantaloup, long, and veinless, with the
ratio of coincidence being 0.537. Clark (1942)
reported data from six loci scattered along
about 70 units of the "cantaloup" group thought
to be near the center of the sex chromosome.
These data indicate that the black to lemon
region does not interfere with the lemon to can-
taloup region, but the cantaloup to honey re-
gion does interfere with the lemon to cantaloup
region. In testing the possibility that the
length (23.0) of the black-lemon region might
be responsible for the lack of interference,

the region was compared with a region of similar length (22.3) to the right of lemon, namely, cantaloup to honey. Coincidence for black-lemon, and lemon-cantaloup, was · found to be 1.07, while the lemon-cantaloup, and cantaloup-honey, was 0.28. Clark suggests that the reason for the lack of interference between the black-lemon, and the lemon-cantaloup, regions is that the spindle fiber attachment center is located near lemon. If such is the case, then the region of the sex gene is about 150 units away from the spindle fiber attachment region.

A third group of genes designated as the "red" group (Anderson and P. W. Whiting, 1939) consists of five loci with a map distance of 74 units. This group forms the right end of the sex chromosome. Twelve other genes are also located on this first chromosome. For their position and crossover value see Fig. 17 or Table II.

A second chromosome, or linkage group two (II) of three loci, 35 units in length, has been identified (P. W. Whiting and Benkert, 1934). This linkage group consists of three mutants, kidney, orange, and miniature. A three point experiment planned to determine the relative positions of kidney, orange, and miniature, gave 7.5 per cent crossing over between orange and miniature, and 27.5 per cent crossing over between miniature and kidney, with 2.8 per cent double crossing over. From these data it may be concluded only that miniature lies about one-fourth the distance from orange to kidney (Fig. 17).

The third chromosome, or linkage group three (III), of four loci is approximately 44 units

in length. Carson (1941) introduced three genes, broken, white, and stumpy, in the four possible combinations. Linkage between broken and stumpy gave a crossover value of approximately 25 per cent. While the linkage between stumpy and white gave a crossover value of approximately nine per cent. From these and other data Carson concluded that broken, stumpy, and white, are arranged on the chromosome in that order. The gene, attenuated, since lost, showed linkage with white with 10 per cent crossing over, and with stumpy with 22 per cent crossing over. Its position, therefore, is to the right of white (Fig. 17). Recent work done by P. W. Whiting shows that white and pellucid are very closely linked, only a few recombinations occurring out of several hundred wasps counted. There is also suggestive evidence for linkage between red and white with 41.5 per cent recombination (Helsel, 1942). Further breeding tests will be required to substantiate the evidence. If found valid, the known linkage groups will be reduced to three.

The fourth chromosome, or linkage group four (IV), consists of four known loci and is approximately 63 units in length (P. W. Whiting and Benkert, 1934). The four mutants in this linkage group are shot-veins, small-wings, truncated, and maroon, arranged in this order on the chromosome. Shot-veins and small-wings are linked with a crossover value of approximately 24 per cent. Matings between shot-veins and truncated show linkage with a crossover value of approximately 12 per cent. Maroon and truncated are linked with crossing over approximately 27 per cent.

There are ten genes remaining to be located in the ten possible linkage groups, Table II. At present, breeding tests are being carried on in order to test the presence or absence of linkage among these unlocated genes. New genes are still coming to light. These may prove to be located on chromosomes as yet unmarked, or it may be that they will be found to be linked with known groups. The number of genes that may eventually show up through visible effects is incalculable. Table II shows which genes have been so far tested.

In linkage tests, the x-factor acts as a single gene, occupying a point on the linkage map. The method of making a linkage test with the sex-factor may be illustrated by a single example (P. W. Whiting, 1945b). The mutant gene, fused, lies about ten units to the right of x. An orange-eyed female heterozygous for fused, o.xa.+/o.xb.fu, is crossed with a black-eyed fused male, +.xb.fu. The orange-eyed sons are haploid from unfertilized eggs and are fused and non-fused in equal numbers. Sex-linkage is not determinable among these because xa males and xb males are similar. The black-eyed zygous diploid or biparental offspring o/+, are either fused or non-fused, and either males or females. From the ratio of the different combinations the percentage of crossovers may be determined. In the example given, the non-crossover offspring will be xa.+/xb.fu or non-fused females, and xb.fu/xb.fu or fused males; the crossovers, averaging in this case 10 per cent, will be xb.+/xb.fu or non-fused males, and xa.fu/ab.fu or fused females. This is called a two-allele cross.

In crosses involving three sex-alleles, sex-
linkage cannot be determined because all the
zygous offspring are heterozygous for x and
are, therefore, female; xa/xb X xc gives xa/xc,
xb/xc. Fecundity is higher here, and the ratio
of females to haploid males is doubled because
the poorly viable diploid males are replaced by
females. In this case, if the cross is made
between a female heterozygous for fused and a
fused male, fused and non-fused females are
produced in equal numbers.

Three kinds of fraternities from heterozy-
gous females by fused males are therefore dis-
tinguishable as follows:

	Females	Diploid Males	Haploid Males
	Non-fused fused	Non-fused fused	Non-fused fused
(1) two-allele	9/1	1/9	1/1
(2) two-allele	1/9	9/1	1/1
(3) Three-allele	1/1	0	1/1

Linkage tests involving two or more mutant
types fall into two general categories, (1) re-
pulsion tests, (a X b), and (2) coupling tests,
(a.b X +). The mutant factors may be intro-
duced from different parents (repulsion tests)
or the double mutant type may be crossed with
wild-type (coupling tests). It is advisable to
make these reverse crosses to check deviations
that result from viability differences, but
thus far most tests have been of the repulsion
type as this is the more convenient way to test

new factors. No consistent differences have
been found between F2 fraternities resulting
from reciprocal crosses (a female X b male and
b female X a male in the case of repulsion tests
or + female X a.b male and a.b female X + male
in the case of coupling tests). When two mu-
tant types are female sterile, the female het-
erozygous for one is crossed with the male of
the other, in which case only those F2 frater-
nities containing both mutants are of value.

Unmated females resulting from crosses in-
volving various mutant genes produce males par-
thenogenetically. These segregate in gametic
ratios. Thus a female, o/bl, from a cross of
orange-eyed by black-bodied, shows independent
segregation of these two differences. The four
types of sons, wild-type, orange, black, and
orange-black, occur in equal numbers. The same
result is obtained from the reverse cross fe-
male, +/o.bl, resulting from a cross of wild-
type, by orange-black. Lemon body color and
cantaloup eyes are linked with about ten per
cent crossovers. Thus le/c females produce
males, +, le, c, le.c, in 1:9:9:1 ratio while
+/le.c females give the same types of male off-
spring in reverse ratio, 9:1:1:9. A female may
be heterozygous for several differences produc-
ing more complex ratios. Factor interaction is
shown, as in lemon, honey, and black, body col-
or, giving characteristic and clearly distinct
double mutant types, le.ho, le.bl, ho.bl, and
the triple mutant, le.ho.bl. Masking effects
are illustrated, as when white eyes prevent
other eye color differences from showing. Via-
bility differences appear when some mutant
types are less frequent than wild-type. Dif-

ferent mutant combinations show different de-
grees of reduced viability which may be deter-
mined by relative numbers in counts of segre-
gating fraternities.

Linkage estimates are ordinarily made from
double backcross data. Breeding out virgin
Habrobracon Fl females gives ratios of the type
obtained from a double backcross. The formula
for estimation of linkage is derived by using
the method of Maximum Likelihood (Mather, 1938;
Fisher, 1941). This method leads, in the theory
of large samples, to an estimate having the
smallest standard error which the data will
allow. If P equals recombination fraction, r
equals number of recombinations or crossovers,
s equals number of straights or non-crossovers,
then $P = r/(r + s)$. It must be remembered that
each double recombination represents two cases
of a single recombination and must be added to
the single recombinations in each region to ob-
tain the total amount of recombinations in that
region. The recombination fraction can never
exceed 50 per cent since of the four available
chromatids only two can produce detectable re-
combinations. A higher recombination fraction
indicates that the genes are relatively far
apart; a low recombination fraction, that the
genes are close.

A variation of the formula, $P = r/(r + s)$,
was presented by P. W. Whiting and Benkert
(1934). They let AB, aB, Ab, and ab represent
the frequencies of the four phenotypes of off-
spring expected from heterozygous females a.b/+
(coupling test) or a/b (repulsion test). It may
be supposed that wild-type, AB, is the most vi-
able, but somatic overlapping may increase the

relative number of AB and of aB phenotypes at the expense of Ab and ab respectively, or the reverse may occur. It may also happen that AB will be increased at the expense of aB, while AB is not increased at the expense of ab. This may be the result of the influence of factor B versus b or to a modifier of trait A versus a linked with factor B or b. A factor preventing overlapping acts as a "differentiator" (Bridges, 1919).

AB may exceed aB as the result of differential viability in which case we might expect a comparable excess of Ab over ab. However, the ratio ab/AB cannot be predicted from (aB/AB) X (Ab/AB) since in some cases the double mutant type fails to be reduced proportionally to the single while in others the double may be highly lethal although one or both of the singles may show viability equal to that of wild-type under the conditions of culturing.

Linkage of one of the genes (A or a for example) with a lethal or semilethal may cause an excess or a deficiency of a mutant type of normal viability. Thus aB may surpass AB or the reverse. In this case we may expect a corresponding shift between ab and Ab, but such may not be obvious because of viability differences or somatic overlaps between the various combinations of A and a with B and b, or because of linkage of a second lethal or semilethal with B or b. While lethals are invisible in the material thus far presented on linkage, semilethals may be either visible or invisible. Complete lethals, dying as pupae, which may be identified as to a second trait (eye color for example), have been shown in Habrobracon. Degree

of lethality of a semilethal factor differs
widely under diverse environmental conditions
and in different stocks. This has been shown
in Habrobracon for a number of visible mutant
types of low viability. The mutant genes are
here semilethals which have a recognizable ef-
fect on the surviving individuals. Factors or-
dinarily designated as semilethals presumably
differ from these only because of failure to
find a conveniently visible trait difference
(Schaeffer, 1945). In Habrobracon, with its
haploid males, stocks very quickly become pure
for modifying factors by lethal selection. It
seems likely that a balance of factors should
thus be readily attained tending toward greater
viability. Relatively disharmonic combinations
may be expected to enhance by their cumulative
effect the influence of a semilethal among the
progeny of hybrid females. A larger proportion
of the La/Lb daughters than of the La/Lb sisters
of the hybrid mother might then be inviable.
In five tests involving reciprocal crosses of
two orange-eyed stocks and in one test of one
of these stocks having the loosely sex-linked
gene stubby with a third stock, lethal effects
were present associated with the dominant allele
to stubby. The lethal effect is regarded as
complementary. It is probable that this lethal
factor lies to the right of stubby (Schaeffer,
1945). Another lethal factor (Helsel, 1942)
showing 25 per cent recombination with white
and pellucid has been detected.

In the case of linkage between a and b,
AB/(AB + aB) might be expected to equal ab/(Ab
+ ab) were it not for one or more of the three
disturbing factors--somatic overlapping, non-

proportionate differential viability, and linked lethals or semilethals.

It is obvious that what has been said as to the relations of a and b may also apply to the relations of either a or b with a third factor c, or a fourth factor, d. It is sometimes necessary to make comparisons of pairs of frequencies as regards a and b, separately for groups CD, cD, or Cd since either c or d may affect phenotypic ratios of a or b.

Table I has been prepared in order that the reader may readily estimate the statistical significance of various pairs of frequencies occurring in the summaries of linkage data in Habrobracon literature. By dividing the lower frequency by the sum (n) a percentage is obtained deviating more or less below 50 per cent. (P = .90) are those percentages at or below which 10 per cent of the samples of a given size (n) will be expected to fall, while (P = .99) are those percentages at or below which one per cent of the samples of corresponding size will fall. The reader may then be 90 per cent sure that there is a significant difference from equality between the two frequencies if the percentage is as low as or lower than (P = .90) and he may be 99 per cent sure if it is as low as or lower than (P = .99). Whether these statistically significant deviations indicate somatic overlapping, differential viability, linked lethals, linkage of the two genes under consideration, or some combination of these conditions must be judged in the individual case from the nature and variability of the traits and comparison of the different percentages

with each other and with the relation of the factors in the Fl parent.

Whether there is linkage and what may be the best estimate of the percentage of crossovers cannot necessarily be determined from the ratio (AB + ab)/(AB + aB + Ab + ab). Muller (1916) has shown a convenient method, The Square Root of the Product Method, for determining gametic ratio, recombinations (r) to straights (s), which compensates for viability differences. If viability is affected proportionally by two pairs of alleles, regardless of their combination, and if the numbers of the genotypes be AB, aB, Ab, and ab respectively, the gametic ra-

tio, r/s equals $\left(\sqrt{\overline{AB \times ab}} : \sqrt{\overline{aB \times Ab}}\right)$ for

the repulsion test and $\left(\sqrt{\overline{aB \times Ab}} : \sqrt{\overline{AB \times ab}}\right)$

for the coupling test. If, however, the factors differ in their effects on viability according to their various combinations with each other and if genotypes from the repulsion cross be AB1, aB1, Ab1, ab1, and from the coupling cross AB2, aB2, Ab2, and ab2, then gametic ratio should be equal to any one of the four expressions:

$$\sqrt{\frac{AB_1 \times Ab_2}{AB_2 \times Ab_1}} \quad \sqrt{\frac{AB_1 \times aB_2}{AB_2 \times aB_1}} \quad \sqrt{\frac{ab_1 \times Ab_2}{ab_2 \times Ab_1}} \quad \sqrt{\frac{ab_1 \times aB_2}{ab_2 \times aB_1}}.$$

This second method, the method of reverse crosses, does not compensate for linked lethals, but comparison may be made of the six ratios obtainable (two by first method in case reverse crosses are made and four by second) and in case of differing results presence of linked lethals determined.

Muller's method does not compensate for somatic overlaps or for difficulty in determination of types, in which case phenotypic ratio involves not only deficiency of certain types below gametic ratio but also excess of other types. If viability difference be absent between A and a and if overlapping be from a to A in the same proportion whether B or b be present, then the phenotypic distribution AB, aB, Ab, ab, may be corrected as follows: Decrease AB by subtracting $((AB + Ab - aB - ab)/2(AB + Ab + aB + ab))$ X aB + ab and increase aB by the same amount. Also decrease Ab by subtracting $((AB + Ab - aB - ab)/2(AB + Ab + aB + ab))$ X ab + aB and increase ab by the same amount. In other words each of the two numerically deficient groups should be increased at the expense of its corresponding excess group by a proportion of itself equal to one-half the difference between the sum of the deficient groups and the sum of the excess groups to the total.

The gametic ratio calculated after this correction is made will in case of linkage always give fewer recombination types than the original data. If overlapping of one difference is always in the same direction and unaffected by the other difference or correlated differences, the gametic ratio obtained should be correct. Even if overlapping is in both directions (from

A to a as well as from a to A), recombinations after correction should be fewer than before. True crossover value will not be greater than that indicated by ratio thus obtained, but it may be considerably less. The value of the method lies in the fact that it gives a maximum which is lower than may be calculated from the frequencies directly.

If the percentage of single recombinations is known for each of two regions, the probability of two recombinations occurring simultaneously, one in each region, is the product of the percentage of singles in each region. Theoretically, the percentage of double recombinations observed should equal the product of the percentages of singles but actually, in most cases, the observed double percentage is lower than that expected because of interference. Stevens (1936) has derived the following formula for measuring interference in terms of coincidence using the method of Maximum Likelihood:

$$c = wn/(w + x)(w + y)$$

where c equals coincidence, w equals number of double recombinations, n equals total number in cross, x equals region (1) recombinations, and y equals region (2) recombinations. This formula makes possible the estimation of coincidence directly from the raw data. A coincidence value of one (1) indicates no interference; a value of zero (0) indicates absolute interference.

There is no significant change in recombination percentage because of aging of the female. Coincidence values also show no significant

change because of aging of the female; however, all crosses indicate that the variation of the coincidence value from one (1) is less in the later vials, but not significantly so.

Chapter IX

ENVIRONMENTAL EFFECTS

It has been found that in Habrobracon ju-
glandis, as in other experimental animals, cer-
tain environmental factors have marked effects
upon the appearance, fecundity, and behavior of
the animal. The nature of mutations and the
rate of their occurrence are also affected. In-
vestigation of various factors and their effects
is at present in progress. Temperature, humid-
ity, and X-radiation, have been found to be im-
portant in developmental studies.

Ever since Habrobracon has been reared in the
laboratory, the degree of temperature has been
known to determine body color, to affect repro-
duction, to affect the production of mosaics,
and to cause mutations. Wild-type individuals
vary from honey-yellow to almost black, higher
temperatures producing more yellow pigment, low-
er more black. Heredity plays some part, for
races under constant temperature differ con-
sistently in pigmentation.

Schlottke (1926) from a carefully planned and
controlled study of temperature and pigment in-
terrelationships in wild-type Habrobracon draws
the following conclusions: (1) deposition of
pigment (black) decreases linearly with rising
temperature; males are on the average, darker
than females, (2) pigment is deposited especial-

ly at points of muscle attachment and the last
parts to become light in higher temperatures
are the regions where muscles attach vertical-
ly, (3) animals bred at lower temperatures are
larger and darker than those at higher, but at
a given temperature the smaller animals are the
darker, and (4) changes in temperature at any
time between egg stage, four days before laying,
and prepupal stage, affect adult coloration. In
a later study (1934) he shows that increase or
decrease of oxygen content of the atmosphere
increases pigmentation; and he concludes that
variation of oxygen concentration influences
the oxidations concerned with pigment formation
indirectly as a non-specific stimulus on the
organism as a whole. Kuhn (1927) has shown by
selection and by crossing that heredity plays a
considerable part in color determination. He
argues for a hereditary cytoplasmic influence.
P. W. Whiting (1926a) has demonstrated linkage
of a gene affecting color of mesosternum with a
gene determining defects in wing vein, R4. An
extensive series of experiments indicates con-
siderable genetic independence of various body
regions as well as both linkage and physiologi-
cal correlation with certain mutant genes.

Despite the great range of variability in
diverse regions of the body, bilateral symmetry
is the rule with very rare exceptions. An oc-
casional defective specimen with asymmetrical
morphological malformation is likely to show
correlated changes in pigmentation. There have
likewise occurred a few specimens with an ir-
regular mottling of color, but this appears to
be pathological. Instances in which specimens
of normal form and non-mosaic for mutant traits

have shown pigmental asymmetry are exceedingly
rare. Observation of specimens mosaic for var-
ious mutant factors and for sex (gynanders),
however, indicate greater or less asymmetry in
body color. A certain quantity of black pigment
in the given region is, of course, a prerequi-
site for visible asymmetry. Total absence of
color resulting from high temperature during
development or to other causes obviously renders
a genetic difference incapable of expressing
itself. Likewise, if environmental conditions
are such that the parts are very black, a rel-
atively slight difference determined genetical-
ly would not be apparent. Females are in gen-
eral less deeply pigmented than males in any
given strain, and consequently gynanders usual-
ly show striking asymmetry in color correlated
with asymmetry in sex.

The pigments of the stemmaticum of Habrobracon
are granular and present in hypodermal cells
beneath clear cuticle. The other pigments, rang-
ing from pale yellow through brown to black, are
in the cuticle and appear to be non-granular.
Both granular and diffuse pigments are similar-
ly affected by temperature changes and undoubt-
edly belong to the melanins. The melanins are
formed from colorless substances or chromogens
with the aid of enzymes in the presence of oxy-
gen. A. R. Whiting (1939b) points out that
Wright's theory of pigment formation in mamma-
lian hair is apparently applicable to the cu-
ticular pigments of Habrobracon. According to
Wright (1917) the colorless chromogen is formed
in the cytoplasm, and two enzymes or their fore-
runners are formed in the nucleus. The union
of these substances in the cytoplasm in differ-

ing amounts and under different conditions gives
rise to different colors and intensities of
color. Chromogen and enzyme I (and O2) are nec-
essary for any color production; acting together
they produce yellow. Enzyme II has no effect
alone, but in combination with I oxidizes chro-
mogen to black and is effective below the thresh-
old of I alone. In the absence of I no color
can be produced, in the absence of II, no black.
Figure 18, is an attempt to express in simple
form the maximum potentiality of each genetic
type in respect to each enzyme. Wild-type is
used as a standard. Quantity of enzyme I is rep-
resented on the left, of II on the right. Any
environmental condition which lowers the ex-
pression of II increases the expression of I.
Lower temperatures change the black pigment of
the lemon mutant less strikingly than that of
wild-type or black. The black areas never be-
come as intense or widespread, but in spite of
this there is a striking lightening of yellow.
This fact taken together with the lighter gen-
eral color at higher temperatures and the ob-
served transparency of thoracic cuticle at both
temperatures suggests a deficiency of enzyme I.
There is too little of I to combine with II to
form as much black as in wild-type and likewise
too little to produce the full amount of yellow
even at high temperatures (A. R. Whiting, 1939b).

The effect of temperature on the eye colors,
carrot, maroon, and the combination, carrot-ma-
roon, has been tested (David, 1938). Limited
experiments have also been made with the eye
color, cantaloup, and with the body color, lem-
on. The temperature ranged from 37° C. to 15°
C. Except for cantaloup, which showed little
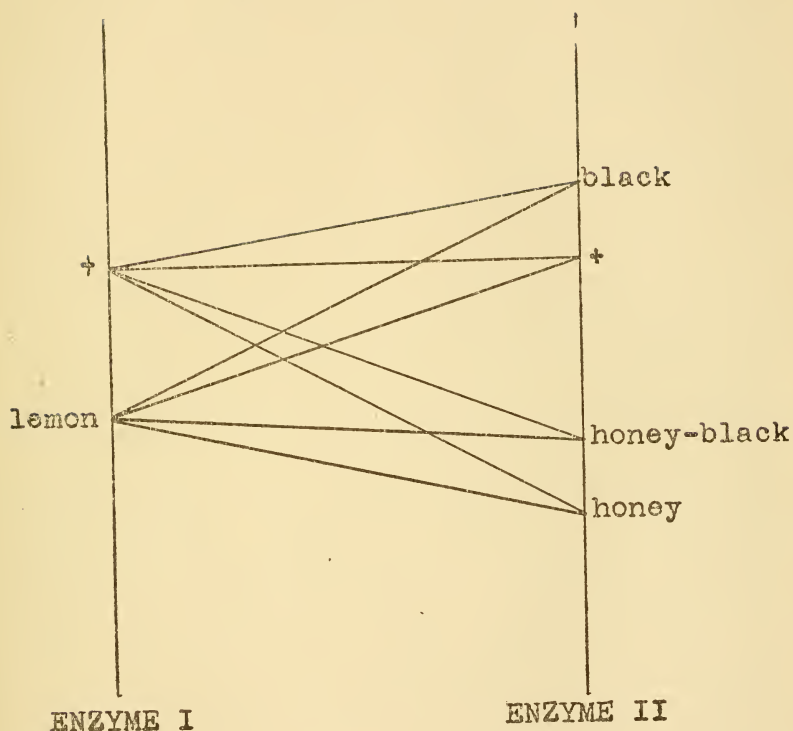
Fig. 18. Relative potencies of
enzymes I and II in each genetic
type. A. R. Whiting, 1939b.

if any change, the intensity of the eye colors varies inversely with the temperature, in contrast to that of body color (type and lemon) which varies directly with the temperature. Carrot showed wide variation from white at low temperature to a deep reddish carrot at high temperature, maroon showed less variation, from a bright red to a dark red or black, and the combination, carrot-maroon, showed still less variation from white to pale yellow. White-eyed carrot wasps were phenotypically like genetically white-eyed. The bright red of the maroon was similar to the deep reddish orange of the carrot. Body color is determined earlier in development than is eye color.

Temperature treatment affects fecundity although short time exposure to cold has only a slight effect. Constant high temperature decreases fecundity by a little less than a third and constant low temperature lowers it to less than half that of control wasps. Constant cold and extreme heat both have very significant effects on fecundity though they apparently act in different ways. Cold acts by slowing down all the activities of the adult wasps thereby decreasing the rate of egg production. Cold also keeps many of the eggs from hatching and kills many of the young larval wasps. Heat treatment apparently has little or no effect on rate of egg production. It affects the young, the consequences being especially noted in the pupal stage. There are many naked pupae and many dead in the cocoons.

Maercks (1933) investigated the influence of temperature and relative humidity on the eggs of Habrobracon. He found the optimal tempera-

ture for hatching to be 29° C., the optimal relative humidity, 80 per cent. The time required for hatching is increased by lower temperatures but is not noticeably influenced by relative humidity except at 19° C. and below, when lower relative humidity slows up development. At optimal temperature egg mortality is not significantly influenced by relative humidity; at low or high temperature it is increased by low relative humidity; at optimal relative humidity it is low through a wide range of temperatures (16-35° C.) but rises quickly to 100 per cent near the lower and upper limits (12° C. and 38° C.).

Temperature treatment of mated females slightly affects the sex ratio of offspring, the most significant decrease in female ratio being observed at constant low or high temperatures. Short time exposure of heterozygous females to extreme cold does not significantly affect the rate of production of male mosaics and gynanders. However, when such females are placed at a constant low temperature, no mosaic offspring appear. On the other hand if females are kept at 35° C. to 37° C. a significantly greater number of mosaics appear (Greb, 1933c).

Experiments with crosses of closely related stocks show that the percentage of diploid males decreases as culture temperatures are increased (P. W. Whiting and Anderson, 1932). Females mated with related males produce fewer biparental offspring if kept at 30° C. than if kept at 20° C. However, at the higher temperature, the percentage of diploid males is greater. Transfer of young to other temperatures appears to have no effect on ratios except that the ratio of biparentals is increased if transfers are

made from 20° C. to 30° C. or 35° C. This is
probably to be explained by a differential le-
thal effect on males in general. At all temper-
atures percentages of males among biparentals
change significantly with increasing age of
mothers. An experiment in which eggs were count-
ed showed that at the higher temperature the
percentage of eggs producing impaternate males
was decreased. Among biparental offspring males
were increased and females correspondingly de-
creased.. The conclusion is drawn that increased
temperature increases mortality of males and
favors homeosyngamy (male-producing combina-
tions) at the expense of heterosyngamy (female-
producing) (Anderson, 1935, 1936). On the whole,
however, sex ratio is less dependent upon tem-
perature than is fecundity.

High temperature may cause or, at least,
bring to light, various mutations. The mutant,
shot-veins, a semidominant factor, appeared ac-
cidentally. It arose simultaneously in three
different lines after extreme heat treatment of
larvae. It causes veins of the wings to be bro-
ken up and distorted. The trait proved to be
hereditary, and shot-veins is fully fertile and
stable.

A number of mutations have occurred following
X-radiation in Habrobracon. Treatment is given
at various stages, to eggs in the mother before
they are laid, to eggs after laying, to larvae,
to pupae, and to sperms in the adult male before
mating. The offspring of the treated wasps are
examined, and the unusual individuals are al-
lowed to produce progeny to show whether or not
the questionable traits are hereditary.

Unlaid eggs of Habrobracon are most sensi-

tive to irradiation in late metaphase I, almost
equally so in latest prophase I (diakinesis) and
least so in prophase stages before diakinesis.
Adult (haploid male) survival from unfertilized
eggs laid by treated females is used as the
criterion (A. R. Whiting, 1939a, 1940a,c).

Hatchability percentages of unfertilized
Habrobracon eggs X-rayed in late prophase I with
doses up to 400 R units are significantly high-
er than those of controls, and the lethal dose
is about 35,000 R units (A. R. Whiting, 1941).
Eggs treated in late metaphase I are sensitive
to 50 R units, and the lethal dose is about
1,250 R units. There is no evidence of recovery
in this stage. The dose-hatchability curves of
the two stages differ, that of metaphase I show-
ing a linear relationship to dose. In 1942 (A.
R. Whiting, 1942a) evidence against "physiolog-
ical effect" as an important factor for meta-
phase I sensitivity was presented as well as
preliminary cytological observations.

Two criteria for judging injury are used (A.
R. Whiting, 1945a). One of these, hatchability,
gives degree of lethal effect, both dominant and
recessive, and is a very accurate measurement in
Habrobracon where unfertilized haploid eggs are
capable of development, where every egg can be
accounted for, where the ideal environmental
conditions are known and easily controlled, and
where there is available a stable wild-type
stock consistently giving 96 per cent hatchabil-
ity or higher. The second criterion, chromosome
changes in successive stages of the treated oö-
cytes, is less satisfactory because Habrobracon
chromosomes are too small (1 u in diameter) for
very careful analysis. Giant salivary chromo-

somes are lacking. Enough has been learned from cytological observation, however, to make this method of some value in connection with hatchability data. The chromosome aberrations observed are necessarily gross ones and undoubtedly represent lethal effects in most cases.

Unmated mature Habrobracon females, when well-fed on host caterpillars and restrained from ovipositing for several hours by removal from host, store in each of their four egg sacs from two to five fully mature eggs which may be retained for at least thirty-six hours without injury. After a much longer period of storage they undergo resorption. They are all in late metaphase I with spindle attachment regions separated and about half way to the poles. The ends of the dyads are still in contact so that the chromosomes appear to be under tension. Occasionally, an egg in late diakinesis or in early metaphase I can be seen entering an egg sac. Successively younger prophase oöcytes occupy the ovarioles anteriorly. Synapsis occurs as soon as the youngest oöcytes can be distinguished from oögonia. An ovariole is represented semidiagrammatically in Fig. 19.

Dominant lethal effects are induced in all eggs treated in metaphase I at about 1,000 R units, in spermatozoa at 10,000 R units, and in eggs treated in prophase I at 45,000 R units. Spermatozoa are not actually inactivated by doses much larger than 10,000 R units. Eggs are also not inactivated by doses much larger than lethal since they continue meiotic phenomena under such conditions. These facts strongly support the theory that the sex of the cell has nothing to do with its response to X-rays but
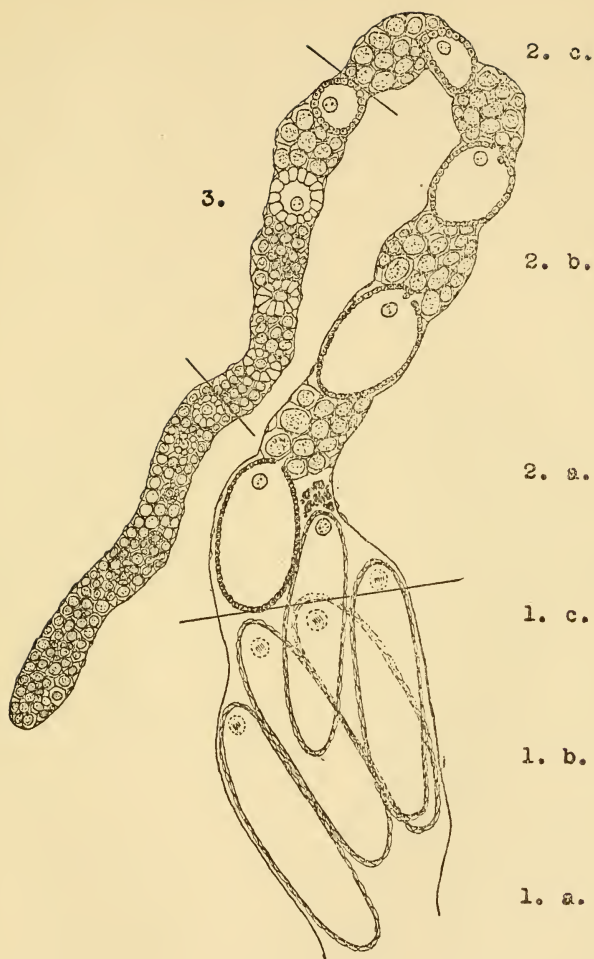
Fig. 19. A single ovariole (semidiagrammatic) showing regions used in classification of treated eggs; 1a, b and c include eggs in metaphase I stored in egg sac; 2a, b and c include eggs in metaphase I, late and mid prophase I; 3 includes eggs in early prophase I. All are post-synaptic.   A. R. Whiting, 1945b.

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rather that the condition of the chromatin de-
termines cell sensitivity.

The extreme and unexpected sensitivity of
metaphase I in Habrobracon oöcytes has caused
some investigators to suggest that the effect
is "physiological" and not the result of direct
chromosome change. It has been found that hap-
loid (male) larvae are more sensitive to irra-
diation than diploid (female) larvae of Habro-
bracon, as expected if chromosome change is re-
sponsible.

Eggs treated in metaphase I and in prophase
I all have chromosomes and fragments, when pres-
ent, distinct in outline in stages following
oviposition and no fusion bridges have been
seen. Absence of a low dose threshold for in-
jury and absence of a high one for clumping and
retardation of meiosis and early cleavage fur-
nish additional evidence against any serious
"physiological" effect in this stage. Since both
metaphase I and prophase I eggs, after their re-
spective lethal doses, present the same pattern
in regard to degree of development before death,
causes of death would appear to be of the same
nature for each.

The linear proportionality between dose and
hatchability as well as the other facts about
metaphase I oöcytes outlined above can be ex-
plained by the following hypothesis (A. R.
Whiting, 1945a). At the time of treatment, dy-
ads are under tension since spindle fiber re-
gions have started toward the poles while ends
are still held in contact by chiasmata. When a
hit breaks a pair of chromatids (a dyad) proxi-
mal to a chiasma the parts will separate, too far
to rejoin but not far enough for the fracture to

be seen. Subsequent complete terminalization
and separation of dyads in anaphase I leaves
fragments and there are no bridges. A broken
dyad produces a bridge in division II in either
spindle with equal frequency. If a single chro-
matid is broken the fragment remains attached to
its uninjured partner and appears in division
II. An egg with a single deletion will fail to
hatch if unfertilized, and, even if fertilized,
when the deletion is large.' If two chromatids
in a "lug" (distal to chiasma) were broken and
the chromatids fused laterally, an occasional
bridge in division I might be expected. Tension
is much less in this region so that restitution
usually occurs when a hit causes a break in
this short length of chromosome. As explained
above, an egg with one double fragment has one
chance in two of hatching, an egg with two such
fragments, one chance in four (if the possibil-
ity of two breaks in one dyad be left out of
consideration).

In Habrobracon, bridges in division II fol-
lowing treatment in late metaphase I cannot be
explained by chromosome splitting following
breakage in view of the structure of the meta-
phase tetrad. It therefore seems probable that
a single hit has broken two chromatids in late
metaphase I. It is known that many deficiencies
are viable in the heterozygous condition, le-
thality being dependent on gene content of the
segment lost. Since diploid larvae are most re-
sistant to irradiation than haploid, recessive
deficiencies must be induced in somatic cells.
It is surprising, in view of these facts, that
all the lethal effects of irradiation appear to
be dominant. If breaks proximal to the chias-

mata are the ones which tend to be permanent, these would necessarily result in large (and therefore dominant) terminal deletions. Deletions small enough to act as recessives might not have a lethal effect on the haploid embryo until after hatching and therefore would not be detected with methods used in present work. In the limited tests made with fertilized eggs it is also possible that a few deficiency heterozygotes surviving would not noticeably affect hatchability ratios.

Genetic literature includes much discussion of lethal factors. In Habrobracon the occurrence of dominant lethals in the sperm can be readily distinguished from direct killing of the male gametes. The most striking result of X-radiation of males is, however, the production of sterility (or partial sterility) of a second type. In this case the sperm are not inactivated but are fully capable of fertilizing the eggs. Such fertilized eggs, however, do not hatch because the sperm have a dominant lethal effect. Females mated to males with this type of sterility produce azygous sons only and in numbers equal to those produced by females mated to normal males; in other words, although they produce no females, as the result of dominant lethal effects of the sperm which have entered the eggs, they behave like mated rather than unmated females in respect to number of azygous sons. Habrobracon, then, is especially well suited for separating dominant lethal male sterility from sterility resulting from inactivated sperm on the basis simply of numbers of azygous sons produced by females mated to the males to be tested (P. W. Whiting, 1938a,b).

As to the nature of dominant lethals it is probable that they are the result of extensive chromosomal alterations rather than to changes in restricted regions or in single genes. A lethal effect from a single gamete may be called dominant in contrast to a condition which must be present in both gametes and hence recessive.

Since in Habrobracon an unfertilized egg provided with a single set of genes develops normally into a male and since the addition of a second complete set by fertilization likewise results in normal development into a female, it might be thought that the addition of a deficient set should not be lethal to the resulting zygote. In other words, if both 1n and 2n may develop normally, why should not 1n + (n-x) also develop normally? The explanation is doubtless to be found in genic balance. If n-x is too small to act as a recessive, containing relatively extensive deletions for example, the balance should be so disturbed that development would be prevented. Theoretically the genic set in a sperm might become so extremely deleted by X-radiation that the fertilized egg would develop as an unfertilized egg into a male. No sex intergrades have ever been found in the treated material that might be interpreted as hyperploid males or hypoploid females. The sex types surviving after X-radiation have been fully as normal as in untreated stock.

Recessive lethal (or semilethal) factors may be a cause of "bad eggs" (P. W. Whiting, 1929a; Maxwell, 1935). Half of the unfertilized eggs of a female heterozygous for a recessive lethal do not hatch. Eggs may likewise be defective in their gross morphological or non-nuclear as-

pects because of unfavorable cultural conditions
(very low humidity) or inadequate nutriment of
females (feeding with honey instead of caterpil-
lar juice) while females of certain genetic
types lay withered eggs of irregular form. Non-
hatchability may then be the result of non-nu-
clear causes, recessive lethals, dominant le-
thals, or male-producing fertilization (P. W.
Whiting, 1938a,b).

Dominant lethals may be induced in the sperm
of Habrobracon by X-radiation of the males. At
10,000 to 20,000 R units all sperm have at least
one lethal. With very high dosages, 41,000 to
142,000 R units, some sperm are directly inacti-
vated while many still remain active and able
to carry dominant lethals into the eggs (P. W.
Whiting, 1937a,b). Neutrons have also been shown
to produce dominant lethals (P. W. Whiting,
1936), being actually much more effective than
X-rays. Ultra-short (1 meter) radio waves ap-
pear to be ineffective (P. W. Whiting, 1937a,b).

Biparental males have been obtained (Stancati,
1932; Bishop, 1937) after X-radiation of sperm
from related males, but the data are not suffi-
cient to indicate their decrease. X-radiation
of sperm from unrelated males has never resulted
in biparental males. Experiments from crosses
with closely related males (treated and untreat-
ed) indicate that while the number of haploid
males produced per day is not changed by X-radi-
ation of sperm, both kinds of biparental off-
spring (males and females) are decreased with
increasing dosages and that they are decreased
at approximately the same rate. This indicates
that X-radiation of sperm fails to modify the
type of fertilization and that the changes in-

duced in the sperm are just as lethal to the biparental males as to the females (P. W. Whiting, 1938a,b).

If females are treated and subsequently mated, there is no appreciable reduction in male ratio, indicating that few, if any recessive lethals are induced in the egg. While treatment of mated females causes a radical lowering of female ratio indicating that more dominant lethals are induced in the sperm than recessive lethals in the egg. It has also been noted (P. W. Whiting, 1929a; N. C. Bostian, 1931) that the percentage of female offspring from X-radiated mothers, mated previous to treatment, is markedly decreased (Greb, 1933).

P. W. Whiting (1937a) demonstrated that treatment of sperm with X-ray dosages of 20,000, 40,000, and 75,000 R units produces at least one dominant lethal in every sperm cell. No daughters occur in the progeny and the average number of males produced per day does not equal that to be expected from virgin females, indicating that many eggs are fertilized and die. Sperm treated with 75,000 R units fertilized almost as many eggs as untreated sperm; therefore, the treatment apparently did not cause inactivation. However, a slight increase in the average males per day from mates of males treated with 75,000 R units as compared with those from mates of untreated controls suggested the possibility that spermatogenesis might to some extent be stopped and sperm supply decreased.

Thus partial male sterility results from dominant lethals at relatively weak dosages, complete male sterility results from dominant le-

thals at stronger dosages, and partial sperm inactivation at very high dosages.

Treatment of Habrobracon larvae with X-rays was begun in January 1929. Progeny from crosses of different stocks were used with pure stocks sometimes treated as checks. Treatments ranging from 730 to 4378 R units were given. No treatment had complete lethal or sterilizing effect, although the highest dosage approached this. Younger larvae were found to be more susceptible to X-radiation than older, and male larvae more susceptible than female larvae. Irradiation tended to kill the younger larvae immediately while the older ones continued development and often died after metamorphosis and before eclosion (A. R. Whiting and Bostian, 1931).

There have been some fifty mutant types derived from X-ray experiments on Habrobracon. Dosages of 2,000 to 5,000 R units have produced the majority of these mutations. After 10,000 R units there is a dominant lethal change of some sort produced in practically every sperm cell. Dosage for egg cells must be much higher for the chromosomes are not so closely packed together and apparently the closer the packing the better chance for irregular recombinations. Table III has been prepared to summarize the effect of various dosages of X-rays on eggs, sperm, and larvae. Considerable experimentation is still being carried on along this line, and various dosages of X-rays are now being combined with treatment at various degrees of temperature.

Chapter X

CONCLUSION

The body of information assembled thus far
establishes Habrobracon juglandis as a genetic
animal of unusual merit. In addition to its
possession of all the prerequisites for a ge-
netic form it has the advantages offered by par-
thenogenesis. Since the normal males are hap-
loid, their genotypes are phenotypically ex-
pressed; thus the need for the traditional back-
cross is eliminated. While it has been shown
that a considerable amount of information has
been accumulated along various lines, in no case
is the knowledge complete, and numerous avenues
of research are open for investigation.

Habrobracon has ten pairs of chromosomes.
Only four and perhaps fewer than four are as yet
known; so that at least six await exploration
and mapping. Many mutations have come to light,
but unpredictable numbers await the chance to
show their effects in haploid males. Numerous
mutations have occurred whose effects are le-
thal to their owners; these when linked with
non-lethals may disturb expected ratios in such
a manner as to betray their presence. These may
be located on given chromosomes.

Regarding the development of the mutants,
very little is known. They are known in their
final adult form, but exactly when and where

deviation from normal development takes place is yet largely a mystery. In some mutants, there is a suggestion of accompanying differences in behavior. These remain to be studied.

Sex determination in Habrobracon has been shown to be complementary, but further experiment is necessary before this hypothesis can be shown to hold for the Hymenoptera in general. The effects of environmental changes, X-radiation, and neutron treatment are being tested, and these are bringing up new questions. All these problems await investigation, and their solution holds promise of interesting and significant contributions to the field of genetics.

APPENDIX

TABLE I

Percentages deviating below 50 per cent with probability
equal to .90 or to .99 that true value is no lower
in population from which sample of a given size,
n, is taken. (Whiting and Benkert, 1934)

n	27	32	37	42	47	55	65
Per cent (P.90)	35	37	37	38	39	40	40
Per cent (P.99)	27	29	30	31	32	34	35

n	75	85	95	110	150	170	190
Per cent (P.90)	41	41	42	42	44	44	44
Per cent (P.99)	36	36	37	38	40	40	41

n	250	350	450	550	800	1500	2500
Per cent (P.90)	45	46	46	47	47	48	48
Per cent (P.99)	42	43	44	45	45	47	47

TABLE   II

HABROBRACON

LINKAGE   GROUPS

LEGEND

☑ Independent assortment
🄽 Crossover percentages
☐ Mutants not yet tested

TABLE III

X-RAY RESPONSES OF HABROBRACON

Dosage	Sperm	Metaphase I Egg	Prophase I Egg	Larvae	Adult
50 R	Viable	Approx. 15% killed	Viable	Young killed	Viable mutations
1,400 R	Viable	Approx. lethal dose	Decline in hatchability	Old active	Viable mutations
2,500 R	Dominant lethals	Meiosis and cleavage	85% hatch	Old pupate	Viable mutations
4,050 R	Dominant lethals	Meiosis	78% natch	Approx. Lethal dose 4,378	Viable mutations
10,000 R	98% Dominant lethals		60% hatch		
20,000 R	100% Dominant lethals		20% hatch		
25,000 R	100% Dominant lethals		12% hatch		
35,000 R	100% Dominant lethals		Lethal dose 44,800 R		
200,000 R	Still active		All killed		
250,000 R					Still alive inactive
300,000 R					All killed

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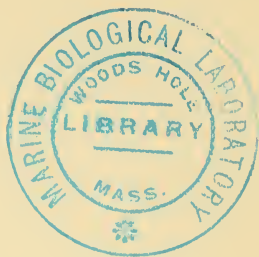
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GLOSSARY

GLOSSARY OF TERMS MOST COMMONLY USED IN HABROBRACONOLOGY

A

ALLELE, one of two or more ·alternative heredi-
tary units or genes, or of the characters
associated with the genes; for example,
the gene responsible for orange eyes in
Habrobracon is an allele of the alterna-
tive normal gene for black eyes (Synony-
mous with ALLELOMORPH).

ANDROGENESIS, development from a sperm.

AROLIUM, an appendage between the claws of
insects.

ARRHENOTOKY, production of impaternate males.

AXILLA (AXILLARIES), the articular sclerites
of insect wings (excepting the tegula,
which is at the front edge of the wing-
joint).

AZYGOUS MALE, male produced by haploid arrhe-
notoky in the regularly established par-
thenogenesis of Dzierzon's Law.

B

BACK-CROSS, the mating of a hybrid to one of
the parental varieties or species which
produced the hybrid.

C

CALCANEA, largest segment of the insect foot, frequently designated the metatarsus.

CENTROMERE, a definite region of a chromosome which takes the lead in activity during mitosis and meiosis. It is the point of spindle-fiber attachment.

CHARACTER, a term used to designate any structure, function, or trait of an organism. A Mendelian character represents the end product of development, in which a particular gene has a specific effect.

CHIASMA, cross-like figure formed by chromatids in meiosis.

CHORION, tough shell or covering of the insect egg.

CHROMATID, either one of the two identical strands into which a chromosome splits in anticipation of cell division.

CHROMOGEN, a substance that under proper conditions may give rise to color.

COINCIDENCE, the ratio of the actual number of double breaks to the expected number of double breaks which should occur if there were no interference.

COSTA, the first principal insect wing vein. It constitutes the anterior edge of the wing.

CROSSING-OVER, the interchange of blocks or chains of genes between two homologous chromatids; also applied to characters which show recombination as a result of such exchange.

CUTICLE (CUTICULA), firm layer outside the hypodermis which protects the insect body and serves as a support for the internal organs. Formed from chitin.

D

DELETION, the loss of a chromosomal segment.

DIAKINESIS, the final stages of meiotic prophase in which the homologous chromosomes are in intimate association.

DIFFERENTIATOR, a factor that prevents somatic overlapping of traits.

DIPLOID, referring to the double set of chromosomes, as found in the body cells of animals and the sporophyte generation of plants, as distinguished from the single (haploid) set, found in the mature reproductive cells.

DISPERMIC, an egg fertilized by two sperms.

DOMINANT, a character which appears as the result of the presence of either a single or a double dose of a particular gene, as contrasted with the recessive, which develops only when both members of a pair of genes are alike. Applied also to the genes.

DOUBLES, double breaks in chromatids that occur during diakinesis, and the resulting genotypes, and the individuals possessing them.

DYAD, each of the two chromatids formed from a single chromosome during meiosis.

E

ECLOSION, emergence of adult insect from the pupal case.

ECTOPARASITE, a parasitic animal infesting the outside of its host as opposed to endoparasite, which lives inside the host.

F

FACET, external face of an insect ommatidium.

FEMUR, the third part of the insect leg, following the coxa and trochanter, usually the largest part.

FIRST RADIAL CELL, region of the insect wing enclosed by radius veins one and three.

FLAGELLUM, the terminal part of an insect antenna.

FOLLICLE CELLS, cells surrounding the developing insect egg which are responsible for the formation of the chorion.

G

GAMETIC RATIO, the ratio of all types of eggs produced by a heterozygous female, expressed phenotypically in the male offspring of Habrobracon.

GONAPOPHYSES, the elements that constitute the insect ovipositor.

GYNANDER, an individual, mosaic for sex.

GYNANDROID, an entirely haploid individual which, however, exhibits characteristics of both sexes.

GYNOGENESIS, development from an unfertilized egg.

H

HAPLOID, referring to the reduced or single number of chromosomes, and to the structures and individuals that bear that number, such as eggs, sperms, and, in Habrobracon, azygous males.

HETEROSYNGAMY, union of dissimilar gametes, or gametes with unlike genotypes.

HOMEOSYNGAMY, union of similar gametes, or gametes with like genotypes.

HOST CATERPILLAR, in Habrobraconology, the larva of Ephestia kuehniella.

HYPERPLOID MALES, males bearing more than the normal haploid set of chromosomes.

HYPODERMAL CELLS, cells of the living layer of the insect body wall.

HYPOPLOID FEMALES, females bearing fewer than the normal diploid set of chromosomes.

I

IMMATERNATE, originating from a sperm and an egg whose nucleus has been destroyed.

IMPATERNATE, originating without involvement of male parent or sperm, as the normal males of Habrobracon.

INTERFERENCE, the inhibitory effect of one crossover upon the possibility of another.

INTERSEXUALITY, a condition in which individuals show characters intermediate between those of two sexes.

L

LINKAGE, the tendency of certain characters to remain together in heredity, since the genes responsible for their expression are located on the same chromosome.

LOCUS, the position of a given gene or any one of its alleles upon a chromosome.

LUG, either end of a chromosome.

M

MELANINS, black pigments.

MESOPHRAGMA, the transverse partition between the prothorax and the mesothorax in insects.

MESOPLEURON, the mid-region of an insect pleuron (see PLEURA).

MESOSCUTELLUM, the mid-region of an insect scutellum (see SCUTELLUM).

MESOSTERNUM, the mid-region of an insect sternum (see STERNUM).

METAMORPHOSIS, the series of marked changes through which an individual passes from the egg stage to the adult stage. In insects, complete metamorphosis includes egg, larva, pupa, and adult stages.

METATARSUS, the first segment of the insect foot.

MICROCHAETAE, minute bristles on an insect body. Those on the wings are of particular use in Habrobraconology.

MIMICS, individuals assuming the appearance of individuals with dissimilar genotypes, such as ivory and white eyes in Habrobracon.

MOSAIC, an individual whose body indicates the possession of more than one genotype by the appearance of varying phenotypes in different regions; for example, in Habrobracon, individuals with one white and one black eye occur.

MUTANT, an individual possessing or exhibiting the effect of a changed gene.

MUTATION, a sudden change in a gene resulting in a new hereditary variation.

MULTIPLE RECESSIVE, the genotype or phenotype of an individual possessing the recessive alleles of two or more different pairs of genes; or the individual itself.

N

NURSE CELLS, cells that alternate in masses with the eggs in the ovarioles of Habrobracon and other insects.

O

OCELLUS, a single eye of an insect borne separately from others.

OMMATIDIUM, a single eye of the compound eye of an insect.

OOGONIUM, a descendant of a primordial reproductive cell which will develop into an oöcyte.

OVARIOLE, an egg tube in an insect.

P

PARTHENOGENESIS, the development of an individual from an unfertilized egg.

PATROCLINOUS, having certain characteristics derived from the father, as diploid males in Habrobracon.

PEDICEL, the second segment of an insect antenna.

PLEURA, the lateral divisions of an insect segment.

PRAESCUTUM, the anterior chitinized line of an insect notum, or prothoracic sclerite (see SCLERITE).

PRIMARY WINGS, the anterior wings of an insect.

R

RADIUS VEIN, the vein that forms the distal costal margin in Habrobracon primary wings.

RADIUS VEINS, R1, R3, and R4, are branches of the radius vein.

RECOMBINATION, a new combination of linked characters in an individual resulting from crossing-over in one or both of the parents; also the individual possessing the new combination.

S

SCAPE, the first segment of an insect antenna.

SCLERITE, any definite area of chitinization in the cuticle of an insect.

SCUTELLUM, the posterior chitinized line of an insect notum or prothoracic sclerite (see SCLERITE).

SCUTUM, the central chitinized line of an insect notum or prothoracic sclerite (see SCLERITE).

SECONDARY WINGS, the posterior wings of an insect.

SENSILLAE, the sense organs of touch in insects,
    particularly hairs and cones.
SEX-MOSAIC, an individual that is part one sex
    and part the other. In Habrobracon, sex
    mosaics are part haploid and part diploid.
SIBS, related individuals, particularly brothers
    and sisters.
SINGLES, a term applied to genotypes resulting
    from one crossover, and to the individuals
    possessing them.
SOMATIC OVERLAPPING, the intergrading of one
    phenotype into another so that neither are
    clearly distinguishable.
STEMMATICUM, the triangular patch between the
    simple eyes or ocelli of an insect.
STERNITE, an area of chitinization in an insect
    sternum.
STERNUM, the ventral division of an insect
    segment.
STIGMA, a thickened, opaque spot on the anteri-
    or margin of the primary wing of an insect.
STING, a pointed, hollow, needle-like organ at
    the posterior end of the abdomen in cer-
    tain female insects; for example, bees and
    wasps.
STOCK, organisms reared and cared for for ex-
    perimental purposes.
STRAIGHTS, gametes containing genes in the same
    combinations that were present in the par-
    ents; the opposite of crossovers.
SYNAPSIS, the conjugation of pairs of homologous
    chromosomes in meiosis.
SYNCYTIUM, a mass of protoplasm in which the
    nuclei are free and not separated from
    each other by cell membranes or walls.
SYNGAMY, the union of gametes.

T

TARSUS, the foot of an insect.
TERGITE, an area of chitinization in a tergum
    (see TERGUM).
TERGUM, the dorsal division of an insect segment.
THELYTOKY, production of impaternate females.
TIBIA, the fourth part of an insect leg, fol-
    lowing the femur.
TYPE, the kind of a species most commonly found
    in nature in a given locality; also ap-
    plied to the genes whose effects are ex-
    hibited by such an individual.
TYPE SPECIMEN, a specimen considered to possess
    the characters of a group. In order to be
    classified as belonging to that group, all
    other specimens must exhibit the same
    characters as the type specimen.

U

UTERUS, the lower expanded end of an insect
    egg-tube.

W

WILD-TYPE, the kind of species most commonly
    found in nature in a given locality.

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